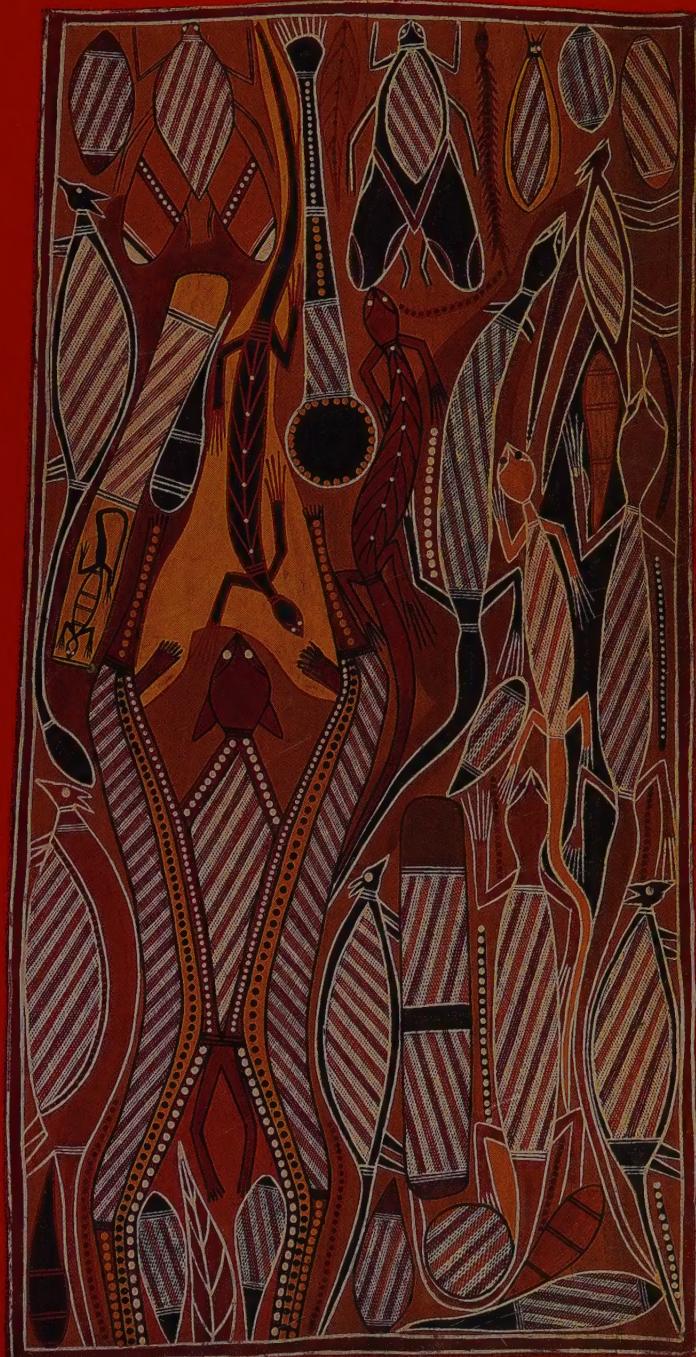




AUSTRALIA

FAUNA *of* AUSTRALIA

VOLUME 1A GENERAL ARTICLES

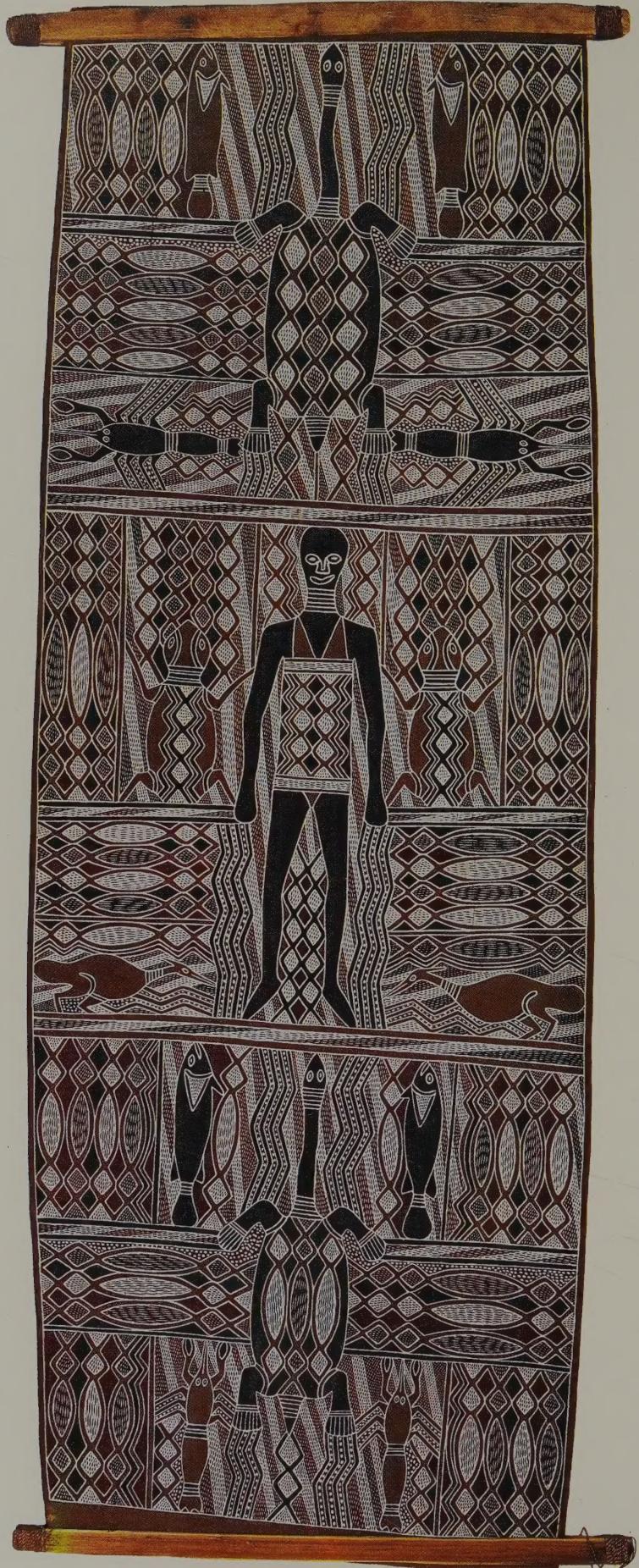


Don Gundinga Djingang (1941–)
Central Arnhem Land, Northern Territory

The artist's totems circa 1979

ochres on *Eucalyptus* bark 122.0×61.5 cm
Collection: Australian National Gallery, Canberra

FAUNA
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Yangarriny Dalwangu (1932–)
Northeast Arnhem Land, Northern Territory
Ancestors of the Yirritja moiety circa 1979
ochres on *Eucalyptus* bark 155.0×56.0 cm
Collection: Australian National Gallery, Canberra

Bureau of Flora and Fauna, Canberra

FAUNA *of* AUSTRALIA

VOLUME 1A
GENERAL ARTICLES



This publication has been endorsed by the
Australian Bicentennial Authority to celebrate
Australia's Bicentenary in 1988

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FOREWORD

The production of the *Fauna of Australia* as an initiative of the Commonwealth Government reflects the deep and varied interests of all Australians in their magnificent and unique island continent. The growing empathy among Australians with their land, its flora, fauna, geographic position and history is a new phenomenon and the decision to produce this summary of present knowledge of the Australian fauna reflects this heightened awareness. The commitment by the Commonwealth Government on behalf of all Australians to bring together current zoological information of an entire continental landmass and the surrounding seas must be regarded as a cultural and scientific event unequalled anywhere in the world.

Australia

What is there about Australia that generates among its people this awareness of magnificence and uniqueness? The answer is easy and simple: Australia is different from every other continental landmass. Defining the nature of this difference is more difficult. How Australia differs comprises much of the content of the *Fauna of Australia*, but a few remarks on the bases of these differences are appropriate here. Australia has had no connection with any other continental landmass for the last fifty million years. Australia has had contact with portions of the Indo-Malaysian Archipelago during this time, but this has always been tenuous. Except to the north, Australia is geographically isolated. In this isolation, the Australian biota to a great extent has found independent solutions to environmental challenges. Since separation from Antarctica, Australia has been geologically stable. Great tectonic events have been largely confined to the leading edge of the Australian Plate, New Guinea. Consequently, an aged and weathered surface covers the continent, with the highest point only two thousand metres above sea level. This has led to soil nutrient levels that are different and lower than those found on other continents. As well, the seas around Australia contain no significant upwellings of nutrient-rich water.

The geographic location of Australia, roughly between 10 and 50° South latitude and 110 to 155° East longitude, gives the potential for a wide range of climatic conditions. Indeed, the Australian climate is variable and, perhaps more importantly, unpredictable. Water is in short supply over much of the continent and this shortage will be a constant thread wherever the terrestrial, freshwater and estuarine faunas are considered.

There are, of course, many other physical factors which have helped determine the character of Australia. The living component of Australia, the flora and fauna, responded to these physical factors and, no doubt, exerted influences on many aspects of the physical environment. As a result of all these features, there exists today in Australia a terrestrial fauna and flora that have large components which occur nowhere else in the world. Though this is less true of the marine fauna, the communities of Australia's ancient and stable southern continental shelf are distinctive. Faunal elements of three major oceans, Pacific, Southern and Indian, impinge on broad stretches of coastline.

The arrival of *Homo sapiens* on the continent is a very recent event in geological time. The emotional expressions of the earliest human accommodation to Australia are recorded in Aboriginal art and folklore. The disorientation felt by early European visitors and settlers is well documented. The effects of the distinctiveness of the continent and its fauna pervade the responses of both Aboriginal and European Australians.

Early written accounts of Australian zoology and botany were recorded by Europeans. These records reflect European scientific thinking of the time, but because the content of these records dealt with a largely unfamiliar fauna and flora, the accounts were often greeted with scepticism or regarded as "curiosities". Mainstream biological thought was almost exclusively Northern Hemisphere in orientation, in the questions asked and those data used. Despite the obvious fact that the revolutionary ideas of Darwin were derived in part from observations in the Southern Hemisphere, the biology of this region largely continued to be a "curiosity" until very recently. The biota of the southern continents and the challenge they pose to biological concepts developed in the north now are being "rediscovered" by the biologists of the Northern Hemisphere.

Whether the volumes of the *Fauna of Australia* will broaden perspectives on biological processes and concepts, only future assessments will determine. Certainly, these volumes will be a tribute to those men and women who have done and who do so much to provide all Australians with a better understanding and appreciation of their land and its fauna.

In the early planning for the *Fauna of Australia*, the decision was made to include a frontispiece in each volume. This would be Aboriginal art which depicted something of the fauna covered by that volume: a representation of the earliest zoology in Australia. In addition to zoology, the art captures one pattern of the integration of the Australian environment with the aesthetic aspects of human life engendered by that environment.

A survey of available knowledge of the Australian fauna carried out shortly before the *Fauna of Australia* project began showed that the preparation of meaningful descriptions of many families would be difficult due to a dearth of information. As a consequence, production of the volumes containing the poorest known groups has been delayed until the 1990's. Meanwhile, strenuous efforts are being made through the Australian Biological Resources Study Participatory Program to improve knowledge of these groups to a level that would allow suitable accounts to be prepared. The preparation of the *Fauna of Australia*, as a consequence, has supplied a useful focus for much zoological research in Australia.

Organization

The *Fauna of Australia* will comprise a ten volume series. In such a division, inequities inevitably result. Some parts of the Australian fauna, and indeed certain aspects of parts of the fauna, are better understood than others. Of some groups, virtually nothing is known. The *Fauna of Australia*, there-

FAUNA OF AUSTRALIA

fore, will not only perform the vital function of setting out what currently is known of the fauna, but clearly demonstrate where significant gaps of knowledge lie.

The *Fauna* will include the description of the Australian fauna, usually at the family level. Included for each group is information on the history of discovery, morphology and physiology, natural history, biogeography, phylogeny, fossil record and economic significance. The taxonomic arrangement used and distribution of the taxa among the volumes are shown in Chapter 13 of Volume 1A. To assemble the information for the 10 volumes, contributions from about 1,000 authors and a large number of illustrators are required.

The geographical regions covered in the *Fauna of Australia* are continental Australia including Tasmania, offshore islands including Macquarie Island, Lord Howe Island, Cocos (Keeling) Islands, Australian External Territories including Christmas Island, Heard Island, Norfolk Island and the Australian Antarctic Territories and the Australian Marine Exclusive Economic Zone.

Editorial Matters

The editorial staff for the *Fauna of Australia* is part of the Bureau of Flora and Fauna. Before work started on the first volume, a *Guide for Contributors* was prepared by the editorial staff. A copy of the Guide is sent to each individual contributor. This document and the efforts of the editorial staff are directed toward the goals of achieving consistency of format and unity in style. All contributions undergo external review prior to acceptance.

Style of presentation is the responsibility of the editorial staff. Scientific accuracy is the responsibility of the contributor.

Every country in which English is the primary language has peculiarities in spelling, idiom and definition which vary greatly in origin. Throughout the *Fauna of Australia*, the *Macquarie Dictionary* serves as the standard for all non-zoological words. Each contributor has the responsibility to ensure that zoological terminology is correct and that the provisions of the International Code of Zoological Nomenclature are followed where appropriate.

Acknowledgements

The fine line-drawings appearing in this and subsequent volumes of the *Fauna of Australia* are a tribute to the body of talented biological illustrators in this country. The Australian Biological Resources Study perceived the need to quantify this valuable resource and has created the first register of Australian biological illustrators. A *Guide for Illustrators* was produced to promote consistency and a high standard of excellence for those artists chosen to illustrate the series.

Participation of many contributors to the *Fauna of Australia* project would not have been possible without the full cooperation of State and Commonwealth wildlife authorities, museums and other research institutions, all of which recognized the necessity of an integrated approach to the exhaustive documentation of a nation's fauna.

To the many individuals who contributed to the technical production of the *Fauna*, particularly the support staff within the Bureau of Flora and Fauna, the editors extend their sincere thanks.

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1. EVOLUTION OF AUSTRALIAN ENVIRONMENTS

L. A. FRAKES, BRIAN MCGOWRAN & J. M. BOWLER*

*Authorship as follows:

L.A. Frakes - Introduction and Early Palaeoenvironments
B. McGowran - Gondwana Breakup: Australia in the Past One
Hundred Million Years
J.M. Bowler - Late Cainozoic Environments

INTRODUCTION

The environments inhabited by plants and animals in modern Australia are many and tremendously varied. These environments have changed over time as they evolved and thus singularly suited types of life have varied. Consideration of the spatial and temporal distributions of ancient environments is appropriate in order to speculate on how changing conditions may have influenced the spatial and temporal distribution and diversification of groups of organisms. For this speculation to be fruitful, the ecologies of modern forms are, of course, most significant.

Limitations of Palaeoenvironment Estimations

Modern environments are defined on a multitude of variables and most parameters can be measured with a fair degree of accuracy. Past environments are known only from indirect evidence preserved in the sedimentary records. Preservation is often imperfect or capricious, so that the environment of accumulation is poorly definable. The degree of imperfection increases with the age of the geological deposit. Parameters of past environments, nevertheless, can be specified, and quantified in some cases, through use of physical, chemical and biological methods, such as the recognition of environmentally significant sediment types and measurements of the ratios of stable isotopes in fossil shell material. With biological data, it frequently is possible to use the ecology of modern species to extrapolate back in time, that is to apply known present day tolerances to ancestral forms and to assess the diversity of past assemblages. In many such studies, the fossil remains of the organisms provide insight into the evolution of environments. A type of circularity of deductions from available evidence, therefore, is involved in the process of estimating palaeoenvironmental variables.

The data of palaeontology are useful in palaeoenvironment estimation only insofar as they are taxonomically meaningful and forms are accurately identified. Constant updating of these types of information is required to ensure reasonable interpretations.

Other limitations relate to uncertainties in dating of fossil material or significant rock types. Reference to the most recent work is essential. Revisions in the age ranges of index fossils and of important assemblages are continually in progress; known forms acquire new significance and newly discovered ones frequently refine correlations in age dating. For regional or continent-wide studies, establishment of penecontemporaneous data-sets is necessary and this is always a problem with geological information, both from the standpoint of precise dating and because of scarcity of appropriate and dated materials. There is no data-set in the geological record comparable with synoptic weather observations.

Generalizing the Specific

The tendency of science to focus ever more closely on minutiae applies in the field of geological reconstruction, has its own value and should not be neglected. To purposely ignore detail can lead to serious error. To understand the evolution of Australian environments, it is necessary to avoid becoming overwhelmed by the details, but rather to see the broad sweep of change. Here we consider the evolution of the environments of an entire continent over a period of several hundred million years and, therefore, seek the overview most compatible with all the evidence.

"Measuring" Palaeoenvironment

Only a portion of geological studies is for the purpose of palaeoenvironmental reconstruction. As a result, much potentially useful information on palaeoenvironments is not sought or is overlooked. Despite this, a great deal is known about the natural history of Australia, at least within the framework of tectonics, sedimentation and climate.

Tectonic history, the history of large movements of the earth's crust, is important to our purposes. Vertical movements result in changes in environment through the effects of elevation on soil formation, temperature, humidity and proximity to the sea. There is also the role of tectonics in raising or removing barriers to migration and radiation of organisms. This latter consideration can be significant in deciphering why certain taxa have occupied certain regimes, but not others, at various times in the past. In this sense, knowledge of the tectonic history contributes to our understanding of palaeogeography and, here, knowing about large horizontal motions (or "drift") of crustal segments is also essential. Reconstructions of regional or continent-wide palaeoenvironments are made. Deductions about palaeoenvironments can best be made directly from investigations of sedimentary rocks in the geological record.

Sediments tell us about weathering and tectonic conditions in the source area from which the detrital materials were derived, about the type and nature of the transporting medium and about the conditions of accumulation at the deposition site. The extent to which environment can be specified depends largely on the sediment type, but also on the means of analysis employed (e.g. stable isotopes, facies analysis, comparison of sedimentary textures and structures with those developed in modern environments). Another feature of a sediment can be most useful: its enclosed biota. Again, comparison with modern forms and their distribution permits one to draw conclusions regarding the past.

Inferences about climate come from consideration of all local input to yield a regional picture or from synthesizing the regional summaries into a continental summary. Details can be derived from the sediment and/or its biological content.

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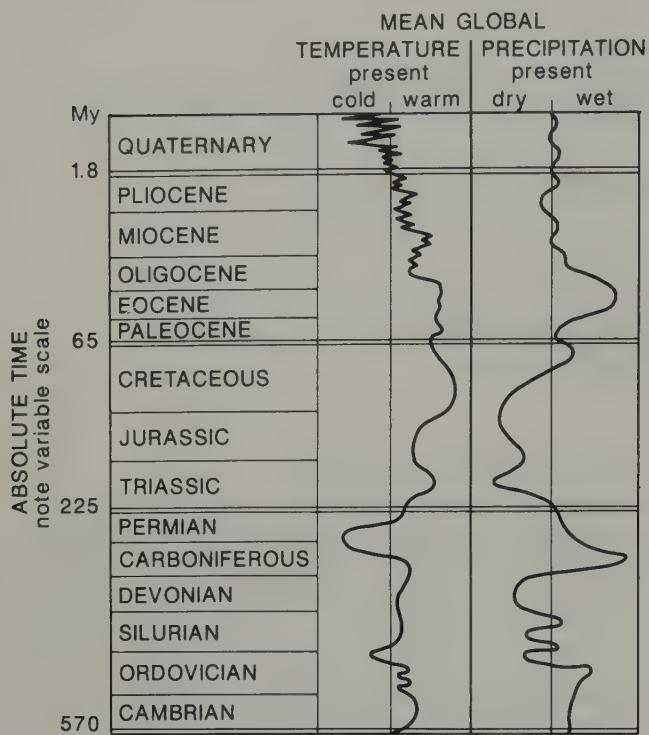


Figure 1.1 Global climate during the Phanerozoic (*i.e.* from 570 mybp to the present). Climate is shown diagrammatically as mean global temperature and precipitation relative to present conditions.
[S. Proferes]

These generally give information about temperature or precipitation conditions and, on rare occasions, even wind or current direction and velocity. An example is the widespread and periodic formation of lateritic soil profiles around Australia over the past 100 million years in response to deep chemical weathering associated with alternating wet and dry seasons.

Because climate is such a dominant influence on local environments, information about past climates is sought widely and climate is the aspect of palaeoenvironment about which there is most often speculation. Most "measurements" of past climate suffer, however, because data are not quantitative, have no basis for comparison with modern measurements (because, for example, fossil forms have no modern analogues) or, in some instances, because modern climates are poorly defined in terms applicable to geologic data. Nevertheless, given the general availability of data having some climatic significance, estimations of past climate are the most useful of geologic evidence in identifying palaeoenvironments and are emphasized here.

The History of Global Climates

Before discussing the evolution of palaeoenvironments in Australia as indicated by evidence of past climates, an outline of the general climatic state of the earth is necessary. For this, we can reasonably consider only that period of earth history for which there is satisfactory stratigraphic control: the last 570 million years, the Phanerozoic. This interval is well represented in Australia by sedimentary rocks in basins of deposition dispersed over the continent (Fig. 1.1).

Climates of the earth have varied sufficiently such that clear indication of variations exist in many parts of the world. Climate change is apparent, both geographically and temporally, from both regional and stratigraphic (vertical) vari-

ations in proxy indicators in the rocks. Examples of change are most evident where change is marked, as in the occurrence of lush subtropical vegetation in Antarctica 100 mybp (=million years before present) or as in glaciation of northern Africa about 410 mybp.

These marked departures from present conditions can be taken to represent changes in the global thermal state. Before the extent of such changes can be estimated, however, determination of the latitudinal positions of the data points as indicated by studies of rock palaeomagnetism is necessary. During the Cambrian Period (about 570–500 mybp) for example, indications from all continents are of warm climates. Although a preliminary glance would favour a uniformly warm earth, palaeomagnetism studies reveal that the continents were disposed not as at present through all the latitude belts of the earth, but rather in a narrow belt between the 40° latitude lines. The evidence for Cambrian climates is thus consistent with past continental positions in low latitudes and the global thermal condition may not have differed greatly from that of the present. Taking account of continental positions, construction of global curves of "average" temperature and humidity throughout the Phanerozoic is possible (Fig. 1.1). Such curves are qualitative and subject to change with new information (compare Fig. 1.1 with Fig. 9-1 in Frakes (1979) for example). Variability in global climates may have terrestrial and extra-terrestrial causes. Most models superimpose fluctuations, caused by variations in atmospheric CO₂ (Greenhouse or anti-Greenhouse effect) or some other terrestrial cause, on the theoretical trend of increasing solar output since the beginning of earth history, because climates of the modern earth are not demonstrably warmer than those of the early earth.

Several factors have influenced the evolution of Australian environments during Phanerozoic time, that is, over approximately the last 570 million years. First among these has been the evolution of the global climate state as a function of both terrestrial and extra-terrestrial cycles and events. Some of these changes have come about directly through changes in the planetary orbit parameters or in the chemistry of the world ocean and the atmosphere, but others have been indirect, involving feedback interactions of atmospheric CO₂, global albedo, tectonic orography and land-sea distributions. Over the Phanerozoic, other environmental changes in Australia can be attributed to changes in the position and orientation of the continent with respect to the earth's spin-axis and to other continents. Thus, over the last 100 million years, as a result of Australia's separation from Antarctica and its migration towards Asia, northern parts of the continent have passed into the tropics after having traversed the temperate and subtropical zones. Southern regions still inhabit the temperate after having left the subpolar zone. New environments, particularly marine ones, were initiated along all the Australian margins except the northern one by the progressive Mesozoic-Cainozoic separation of other Gondwanan fragments: greater India from the northwest and west, Antarctica from the south and the New Zealand-Lord Howe Rise-Queensland Plateau complex from the east.

Australian climates at the beginning of the Phanerozoic, about 570 to 360 mybp (Cambrian to Devonian Periods), were governed by the low latitude (less than 40°) position of the continent, with intermittent reefs growing in Tasmania and New South Wales, sporadic development of carbonate banks in warm shallow seas in Tasmania and the Northern Territory and highly evaporative marine environments in Western Australia, the Northern Territory and South Australia. The dominance of evaporitic basins in the early Paleozoic is not balanced by development of coal basins indicating higher humidity conditions, but this is due at least in part to the fact that significant land plants had not yet appeared on the earth. Other indicators of humid climates, however, are

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lacking and the conclusion must be that in Australia, arid, probably warm, climates prevailed. Throughout most of this interval, the west of Australia lay at lower latitudes than the east and this is reflected in the higher proportion of geologic indicators of warmth in the west.

Between about 360 and 270 mybp (Carboniferous-Early Permian periods), there was fundamental change of Gondwanan climates as a result of the shift of Australia and neighbouring continents into high latitude positions. This led first to the development of mountain and piedmont glaciers in New South Wales and Queensland and subsequent ice sheets affecting all regions, except possibly the Northern Territory. Major ice bodies radiated into Australia from Antarctica (in Tasmania, Victoria and South Australia). There was a concomitant retreat of reef, evaporite and carbonate bank environments beyond the margins of the continent and, where Australia was not glacial or periglacial, it was apparently quite cool. Owing to the construction of large polar ice bodies, global sea-level was low and marine environments were restricted to the continental margins and often associated with volcanism (New South Wales and Queensland).

Also important toward the end of this interval was the spread of the first bog and swamp environments suitable for peat accumulation. Such regimes existed over vast tracts, particularly in New South Wales and Queensland, but also in Western Australia. Earlier, though swamps and bogs may have been common, they were not as widespread and wetlands floras had not yet evolved. Peat swamp conditions persisted until about 250 mybp and then recurred in a broad band stretching from Queensland to South Australia at about 240 to 220 mybp (Triassic). Large fluvial systems developed in association with these environments. The only marine environments on the present continent occupied a narrow area opening off the Indian Ocean in northeastern Western Australia.

Bogs, marshes and large river systems continued as common features of the Australian landscape until late in the Jurassic period when, at about 160 mybp, the continent began to dry. Over this interval of some 60 to 80 million years, Australia lay in fairly high latitudes (40 to 70°) and to poleward of the descending dry air of the subtropical high-pressure systems. Climates of the continent, therefore, reflected moist conditions associated with passing polar fronts. Despite this, however, climates of southernmost Australia (at this time represented by what is now southeastern Australia) apparently were temperate rather than subpolar. Though some desiccation of the continent took place in the Late Jurassic (160 to 140 mybp), humid climates quickly resumed. Meantime, the relative warmth of Australian climates continued.

Elevation of parts of the southern Australian margin, preparatory to separation from the Antarctic landmass, led to development of strongly seasonal climates on elevated areas (120 to 110 mybp). Rivers draining northward from southern Victoria and South Australia into a major interior seaway may well have frozen periodically, but in neighbouring areas, indeed over much of the continent, forests of ferns and podocarps flourished and swamps and marshes were common in Victoria. Other marginal areas of the continent (Western Australia, Queensland) also may have been elevated and, hence, cooler than expected. Between about 100 and 65 mybp there was a widespread withdrawal of the sea, first from the interior and then from the continental margins. Former marine environments were succeeded by fluvial-alluvial conditions, particularly through central Queensland. The latter areas included peat bogs of limited life and distribution. Calcareous nannoplankton proliferated in warm, shallow seas north of Perth, but only for a short interval.

A striking feature of the Australian environments for much of the interval between about 175 and 40 mybp was the extent of the landmass which lay beyond the Antarctic Circle, latitudes greater than about 67.5°S. Surface temperatures were sufficiently warm for the growth of abundant plant life and even for the exothermic reptiles, including dinosaurs in high-latitude Victoria and mid-latitude Queensland. These facts are not explained easily nor is the flourishing of plants at latitudes where long periods of winter darkness obtained.

GONDWANA BREAKUP : AUSTRALIA IN THE PAST ONE HUNDRED MILLION YEARS

In this account of environmental changes at an intermediate scale of geological time, the figure of 100 mybp, neat as it is, also is much more:

- (i) it is close to the Early/Late Cretaceous boundary soon after the last major marine inundation of the continent;
- (ii) it is close to a major "turning point" in geohistory: a recent comprehensive account of Australian geohistory identifies the Cenomanian Interregnum (95 to 90 mybp) as a natural boundary between two successional tectonic regimes;
- (iii) it is close to the beginnings of the record of the angiosperm radiation on this continent;
- (iv) 100 million years quite neatly spans the time of the central problem in global palaeoceanography and climatic changes. That problem is the transformation from the Cretaceous kind of world to the present Neogene situation. The former is characterised by "high mean sea-level, continents low, latitudinal temperature gradients and oceanic vertical temperature gradients low, oceans sluggish and subject to anoxia" (Fischer, 1979). In contrast, the Neogene exemplifies: "low mean sea-level, continents high and mountainous, subject to episodic cover of ice sheets. Latitudinal temperature gradients high, vertical gradients in sea strong, oceans vigorously convective, water masses strongly oxygenated" (Fischer, 1979).

It is as well to be aware from the outset that any account of historical geology has to be written against a background of various beliefs and attitudes. Some of these are as follows:

Change through geological time: Stately sweep or rapid episodic shift? The uniformitarianism of Charles Lyell included not only the notion that the present is the key to the past, in the sense that one can assume securely that water ran downhill then as now, but also that change was gradual. That view has dominated for most of the past 150 years, but now is being supplanted by another old notion which has spent most of its time in limbo: that periods of stability or of slow change are interrupted by periods of rapid change. Alternations of modes are perceived at several different time scales and pertain to seafloor spreading, continental drift and mountain building, to climatic change and to organic evolution. The author (McGowran) made a strong commitment some time ago (McGowran, 1978a) to the now dominant world view.

Episodic or cyclic? Fischer (1984) recognizes two Phanerozoic supercycles: Palaeozoic and Mesozoic-Cainozoic. Each contains a "greenhouse" phase and an "icehouse" phase. Fischer sees the cyclic pattern in sea-level changes, in continental breakup and aggregation and in plutonism, with the cycles based ultimately in mantle convection and in the expulsion of carbon dioxide into the atmosphere. If the Phanerozoic is bimodal, then there may be a cycle with a period of about 400 million years (Fischer, 1984). Fischer &

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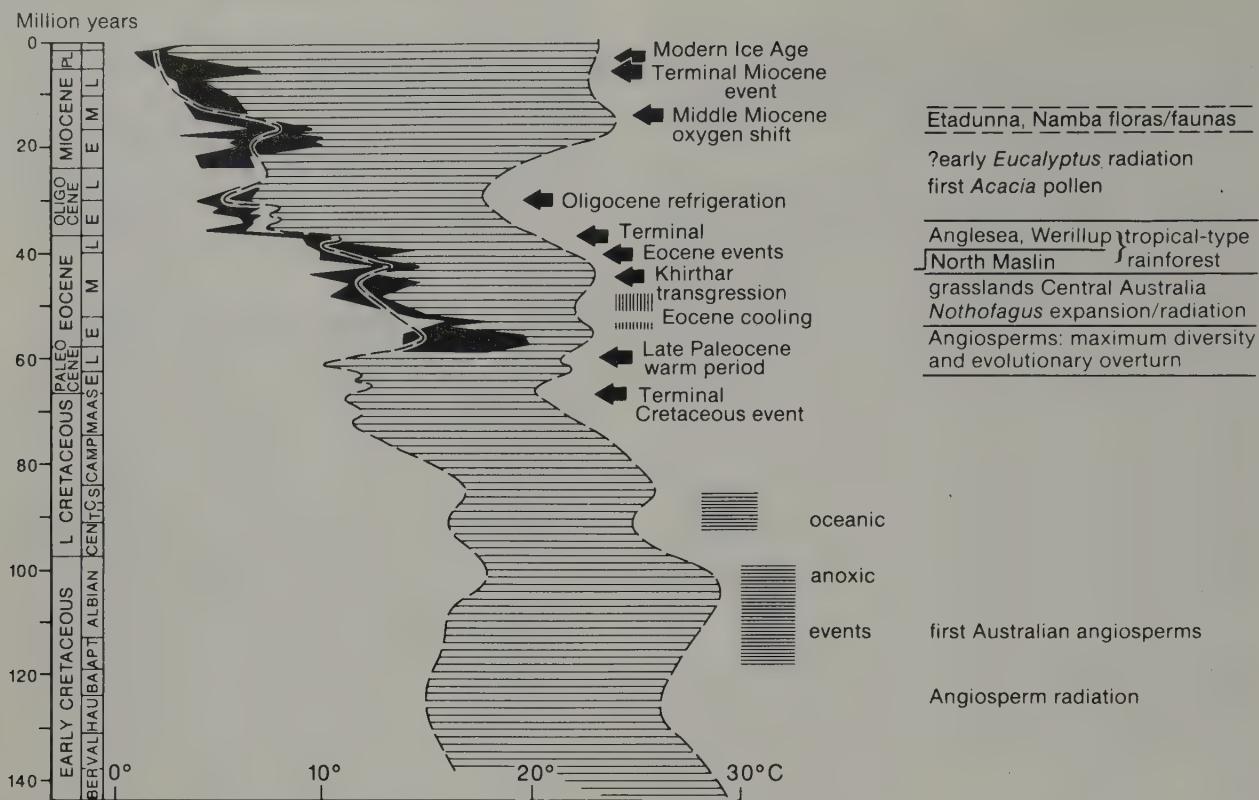


Figure 1.2 Oxygen isotope curves calibrated tentatively against a temperature scale. Shaded envelope covers low-latitude Pacific values (Douglas & Woodruff, 1981) from surface (to the right) values based on planktonic foraminifera and from the bottom (to the left), benthonic readings. The overall trend toward cooling, the reversals and the progressive differentiation between surface waters and bottom waters are all more important than the actual values in °C. Black envelope: high southern latitude oceanic profiles, recalibrated from Shackleton & Kennett (1975). Again, surface to right of envelope, bottom to left. Shading and arrows: events and intervals of global significance. Right: a few records from the Australian palaeobiological succession.

[S. Proferes]

Arthur (1977) recognize overturns in the biosphere at a frequency of ≈ 32 million years. A subsequent statistical analysis of extinctions in the later Phanerozoic revealed a 26 million year periodicity (Raup & Sepkoski, 1984) which stimulated the search – well aired in the popular media – for cosmic cycles. There may be a return in geohistorical thinking to the cycles and periodicities that once were popular, but that have been unfashionable in recent years (Raup, 1984). The clarification of the actual fossil record, upon which all claims of cyclicity and multiple mass extinctions in the biosphere must rest, constitutes the greatest challenge in modern palaeontology. A record sufficiently detailed is not yet available to resolve the controversies that have raged in recent years on speciation and extinction and on the relative influence of endogenic (plate tectonic, volcanic), exogenic (climate, sea-level) and extraterrestrial (comet, supernova, galactic motion) controls.

Local or global? As chronological correlations have improved in reliability and refinement and as studies of geological problems in the later Phanerozoic have progressed, so has it become apparent that local events in earth history tend to be part of an interlocking global history. The obvious examples are: (i) transgressions and regressions as local manifestations of global rises and falls in sea-level; (ii) climate, as manifested in fluctuations in oxygen isotope ratios and thermally sensitive organisms. There are other, and exciting, possibilities in the perception of changes in the chemistry of the global ocean or in the intensity of deep weathering on the continents. The new discipline of systemic stratigraphy (Berger & Vincent, 1981) aims to recognize and correlate global trends, cycles and events through chemical and biological signals. Changes reverberate globally and the event, recog-

nized locally, may amplify or obscure the global signal. It is clear enough that there are numerous "natural" breaks and events in the Australian stratigraphic record and that they are part of the broader tapestry. Signals, particularly climatic signals, are far-reaching, rapid, bipolar and reversible.

Synchronous or diachronous? Deeply embedded in most recent considerations of Australia's geohistory and biohistory is the concept of steady changes as Australia has rafted to lower latitudes. Diachronism, however, is probably a less heuristic notion than the alternative of episodic synchronism and offset allochronous events in a stepped history, with rapid transitions from one geo/biohistorical configuration to the next.

The history that is written as background to Australia's fauna should focus on some aspects whilst blandly neglecting others. Among points of particular importance are:

- (i) the shaping of Australia and its timing depends on Gondwana breakup, which constrains models of biogeographic dispersal or vicariance. Again, breakup was replaced by collision when the continent collided with island arcs in the southwest Pacific after "drifting" northwards;
- (ii) climate, of course, is especially significant;
- (iii) landscape and its evolution depend partly on climate, but underlying that is the tectonism of mountain building and its timing.

The Bare Record of the Late Cretaceous

As outlined above, the last major marine transgression on Mesozoic Australia was in the Albian, whereas global sea-level curves peak later in the Late Cretaceous. Australia was different because of an important natural break in its Cretaceous history, the Cenomanian Interregnum (Veevers, 1984). During this narrow interval of time, a magmatic arc in the northeast became inactive, Australia uplifted en masse and seafloor spreading began between Australia and Antarctica and between Australia and the Lord Howe Rise and New Zealand (the northern, northwestern and southwestern margins of the continent had been formed during an earlier dismembering of eastern Gondwana). In the geohistorical perception and nomenclature of Veevers (1984), the Innamincka Regime gave way to the Potoroo Regime in this cluster of tectonic events. In the sedimentary record the change is marked (a) by the widespread development of unconformity over Albian or Cenomanian strata, (b) by a change in the north, east and southeast of the continent from detrital sediments of volcanic provenance to quartzose sediments derived from the continent or (c) by a change from carbonate-poor to carbonate-rich accumulations on the western margins.

Most of the continent lacks a Late Cretaceous record, the "platform lacuna" (Veevers, 1984). These authors suggest that much of the southern continent drained southwards and that most of the ancestral highlands along the eastern margin drained to the west and southwest, all drainage focusing on the Ceduna Depocentre (beneath the present Bight).

Large tropical-type benthonic foraminifera were able to reach the northern margin (two localities known in the island of New Guinea) at a palaeolatitude of, perhaps, 30°S on the southern shore of the Tethys seaway. The foraminiferal faunas in neritic carbonates on the western margin indicate warm conditions, but not especially so. Quilty (1984) summarizes succinctly the palaeoclimatic evidence for warm moist conditions in the Australia/Antarctica rift. The palynological record in the southeast (Dettmann, 1981) includes indicators of high humidity, cool to mild temperatures and altitudinal zoning. Angiosperm diversity increased and several important elements of the modern austral flora, including *Nothofagus*, were well established by the end of the Cretaceous.

The inferred southeastern highlands have been placed at a floral boundary between warm and temperate ecotones, and between wet and seasonally wet belts through eastern Gondwana (Hallam, 1985). The envelope of oceanic oxygen isotope temperatures (Fig. 1.2) suggests that in the highly equable later Mesozoic world, the oceans were warm, even at depth. Figure 1.2 shows three episodes of global "oceanic anoxic events" (Aptian-Albian, Turonian, Coniacian-Santonian). During those times the oceans accumulated organic carbon, due perhaps to expansion of the oceanic oxygen-minimum layer at higher temperatures (with lowered O₂ solubility) and sluggish circulation (lowered oceanographic gradients). Alternatively, the accumulations may have been due to stagnation of entire ocean basins under salinity (*i.e.* density) stratification when deep water could not be adequately ventilated. This is the world in its greenhouse mode, in which increased levels of CO₂ may be a major control (Fischer, 1982; Hallam, 1985). The fact that extensive "oceanic anoxic events" have not been recognized above the early Senonian is important evidence that transformation to the modern world was well under way during the Late Cretaceous. Indeed, evidence that the terminal Cretaceous extinctions selectively victimized tropical biotas, coupled with palaeobotanical evidence of sharp cooling across the boundary, suggest to Stanley (1984) that temperature change is a prominent proximal cause of marine mass extinction.

The Paleogene Transformation

The Paleocene and Eocene epochs span a truly critical time in the making of the modern ocean. After the "platform lacuna" of the Late Cretaceous, there is a marked improvement in the spread of the Australian geohistorical record and it is necessary to identify and scrutinize several turning points in the passage of that history. For this reason the early Tertiary must receive considerably more attention than the Late Cretaceous in this account.

Figures 1.3 and 1.4 summarize various items of local and global significance. "Global plate reorganization" refers to an interregnum between old and new spreading systems, the change having been brought about by collisions between India and Asia especially, but also by the termination of the quite shortlived episode that opened the Coral Sea. The India-Asia collision forced a subcrustal readjustment which resulted in a new global pattern. The main effects in our region were:

- (i) a rapid increase in Australia's northward motion, after \approx 50 million years of very slow movement; and
- (ii) the greatest of all changes in motion of the Pacific Plate, from a more northerly to a more westerly direction, as seen most clearly in the bend in the Hawaiian-Emperor volcanic chain.

Changes in global seafloor spreading rates correlate in a general way, via displacement of water from ocean basins, with the degree of marine flooding of the continents. The generalized curve (Fig. 1.3) for marine transgressions and regressions over the western margin must be viewed against the overall global fall in sea-level of perhaps 350 m during the past 80 million years (Kominz, 1984). The "sequences", the "cycles" and the curve are seen to be very similar, as indeed they should be. McGowran (1978a; 1979b) and Quilty (1977; 1980) outline cycles/sequences to make the point that some intervals of Cainozoic time are characterised by a relatively widespread and good record (especially marine) on the Australian continent. That record is sparse or lacking for other times. Loutit & Kennett (1981) relate those cycles/sequences to the global supercycles of the "Exxon curve" (Vail & Hardenbol, 1979). Veevers (1984) extends the notion to a comprehensive model of the later (Cainozoic) Potoroo Regime.

In Cycle W, or Sequence One, the first Tertiary transgression reached a modest maximum in the Late Paleocene and Early Eocene with seas on the western and northern margins and sporadic records in the south of the still very narrow South Ocean. Equally significant was the renewal of sedimentary accumulation at various places in the continental interior, particularly in the Birdsville Basin. Jones & Veevers (1982) make a convincing case for two important points:

- (i) trans-Australian drainage to the Ceduna Depocentre was blocked by early Tertiary uplift of the South Australian Highlands, whilst at the same time there was an episode of narrowing and uplifting in the ancestral Great Dividing Range;
- (ii) the rise of sea-level, the subsidence of sedimentary basins and the uplift of highlands to act as source areas for sediment are correlated in time (this more general point is counterintuitive, since one would relate uplift to retreat by the sea, not to its advance).

The Early Tertiary Golden Age

The Late Paleocene and Early Eocene are considered to be a "Golden Age". Warm, humid conditions extended a long way polewards in both Hemispheres. The centre of the Australian continent was moist, with peat-forming swamps and coarse clastic sediments in the Birdsville Basin and smaller basins,

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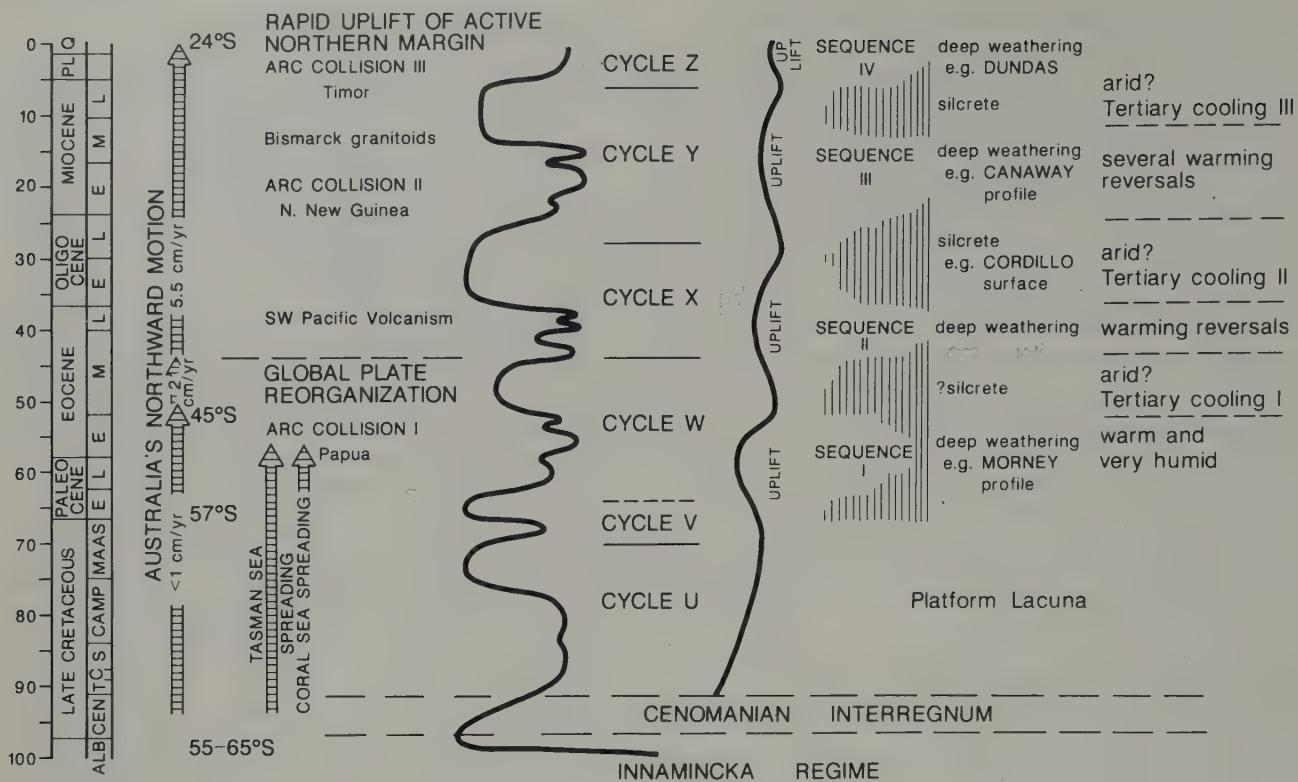


Figure 1.3 Broad and selective scenario of Australian geohistory over 100 million years. From left: (i) Geological time scale; (ii) Plate tectonic events, with major turning points at "Cenomanian Interregnum" and at Middle Eocene "global plate reorganization". Broad arrowheads indicate termination of, or change of rate in, sea-floor spreading; (iii) Sea-level curve for western margin, modified from Vevers *et al.* (1984) (left, low; right, high); (iv) "Cycles" of earth history from Vevers *et al.* (1984); (v) Pulses of uplift and subsidence in eastern highlands, from Vevers *et al.* (1984); (vi) "Sequences" of Australian sedimentary strata and theorised succession of weathering of the landscape, from McGowran (1979); (vii) Main climatic phases: as discussed in text, three phases of cooling/aridity are interrupted by warming/humidity. [S. Proferes]

and palynomorphs of taxa that indicate high rainfall and considerable warmth (see Truswell & Harris, 1982 with references). In an analysis of the relatively continuous palyнологical record in the Gippsland Basin, Truswell (1987) shows that, as indicated by overall diversity, turnover, originations and extinctions, phyto-evolution reached a maximum in the early Tertiary. If the fossil flora at Nerriga near Canberra is of Early Eocene age (Kemp, 1981), then preliminary physiognomic analysis of leaves indicating subtropical rainforest (Christophel, 1981) supports the general scenario for southern Australia at that time.

The isotope palaeotemperature curve illustrated in Fig. 1.4 is based on analyses of oceanic planktonic and benthonic foraminifera. Note that the increasing divergence between surface water and bottom water values at low latitudes during geological time is not matched at high latitudes. Note also, though, that values for the high southern region, palaeolatitude 60° S, overlap low latitude values. This could mean no global temperature gradient (unlikely) or, as Berger (1982) and Berger & Vincent (1981) suggest, the high latitude values "must reflect excess precipitation of ^{16}O -rich rain. The bight between Tasmania and Campbell Plateau (Antarctica and Australia being close together) must have been, on the whole, an estuarine basin with salinity stratification, situated in a rain belt". The rain belt hypothesis fits seductively with widespread evidence for deep weathering, including lateritization, demanding warm, moist conditions. McGowran (1979b) shows that intense deep weathering was coeval and well may have concluded coevally in the high northern latitudes, high southern latitudes and on India at a low latitude. Subsequent episodes of deep weathering certainly occurred (Fig. 1.3), but it is to this major episode, not

the Miocene one, that Beadle's (1981) suggestion – that Australian xeromorphy is a low-fertility adaptation to laterites and deeply weathered profiles – must refer.

The occurrence of broad-leaved, evergreen vegetation at high latitudes ≈ 60 mybp is problematical:

"The conclusion seems inescapable that high latitude photoperiod, including continuous months with little or no daylight, would have rendered unsuitable for mesophytic plants much southern land that palaeobotanists believe was vegetated. The physical evidence is difficult to reconcile with the palaeobotanical view that mesophytic vegetation, with plants whose relatives today are tropical, lived there" (Lange, 1982).

From evidence in the Northern Hemisphere for palms and cycads to latitude 60° N in the Paleocene and Eocene, for crocodilians at $\approx 77^{\circ}$ N in the Eocene and from other indicators of warmth, equability and particularly from the seeming requirement of much more winter light than at present, came the proposal that the earth's obliquity was reduced – perhaps 5 to 15° (*cf.* the present 23°) (Wolfe, 1978; 1980). Creber & Chaloner (1984), however, discuss the importance of ambient temperature, not light, as the limiting factor in plant growth and for good measure invoke increased levels of CO_2 in the atmosphere as enhancing photosynthetic activity as well as warming and ameliorating the climate. Furthermore, Barron (1984) demonstrates, using climate model simulations, that a reduced obliquity may well cool the poles, not warm them. Barron also cites the astronomical difficulties and Conway Morris (1985) buries the theory of reduced obliquity succinctly and convincingly. The problem, essentially and in general terms, is a familiar one in palaeobiology: the physiol-

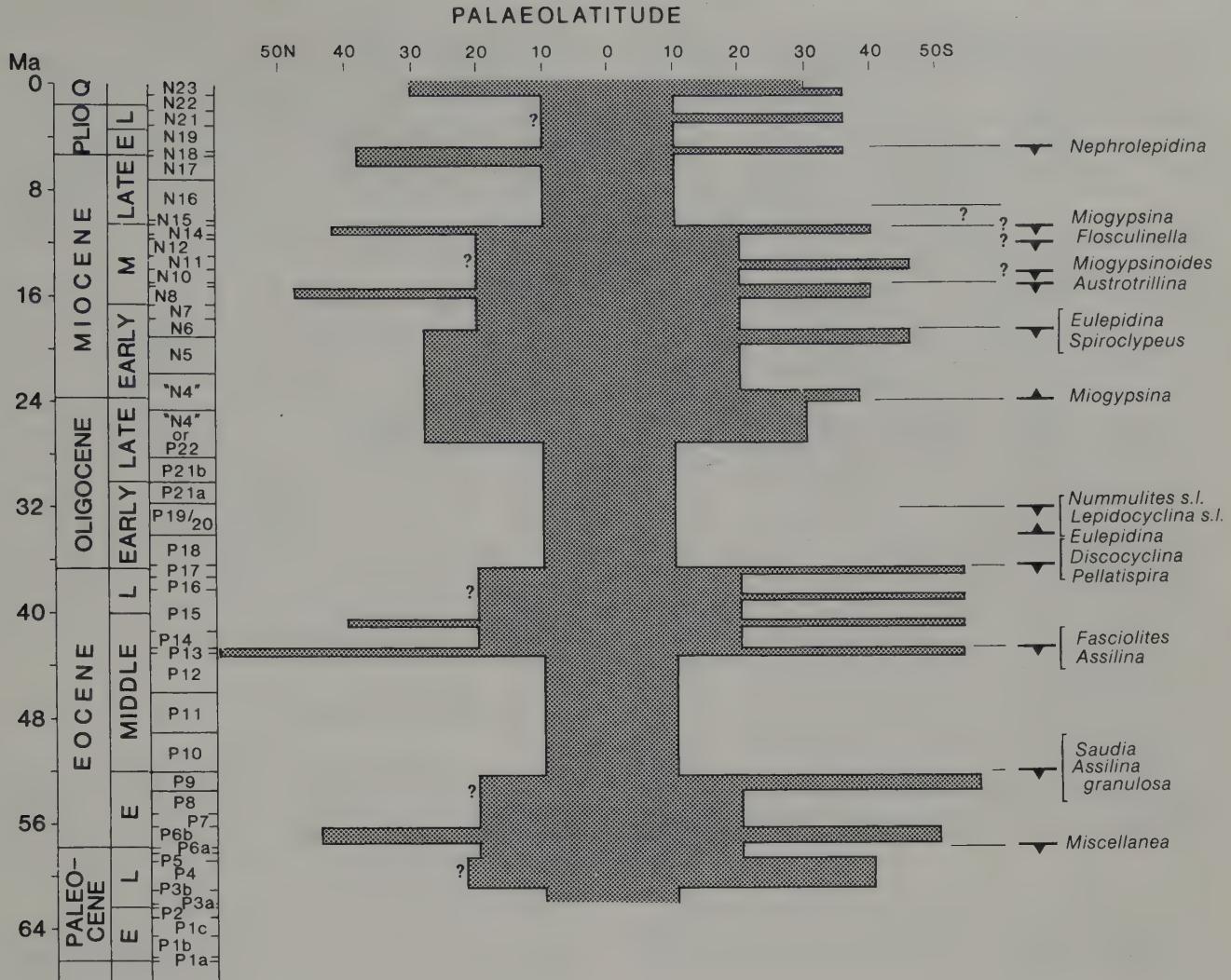


Figure 1.4 A spatiotemporal model, or theory, of the distribution of "tropical", neritic foraminifera, as put forward by McGowran (1986). Some aspects of rapid, shortlived forays to the far north or south are not uncontroversial and the latitudinal widths of the refuges are only guessed at. Even so, one should note that this model fits closely with (i) "Tertiary cooling I, II, III" in Fig. 1.3; (ii) Later Eocene and Early - Middle Miocene warmings in Figs 1.2 and 1.3; (iii) The sense of rapid change from one state to the next, as stressed throughout the text. [S. Proferes]

ogy of modern adaptations is not easily used as a restraint on ancient situations, especially as one gets back into the earth's greenhouse state.

"When the planet next reverts to a Cretaceous climate, it seems more than likely that the forests will return to the Antarctic peninsula, while alligators bask in the long polar summers and hibernate through the tepid winters" (Conway Morris, 1985).

The First Tertiary Deterioration and Later Eocene Reversal

A rapid oxygen isotopic shift across the Early/Middle Eocene boundary south of New Zealand (Fig. 1.4) increasingly appears to be a signal of what is designated "Tertiary cooling I" in Fig. 1.3. This is supported by oceanic micropalaeontological evidence (McGowran, 1977; McGowran & Beecroft, 1985). Berger (1982) takes the decline from the Early Eocene peak to signal the end of the postulated rain-belt effect.

In Australia, a revolutionary change occurred in the flora (Gill, 1975) in which the Tertiary conifer/*Nothofagus* flora replaced the Mesozoic fern/conifer flora. Partridge (1976a,b) records a dramatic increase in pollen of the *Nothofagus brassi* group and the disappearance of "tropical" forms. There seems, however, to be no hard evidence recorded in sediments of early Middle Eocene age in southern Australia (or elsewhere, for that matter, except perhaps offshore Western Australia) (McGowran, 1978a; in press). But that is useful negative evidence in that the hiatus between Sequences I and II is also an interval between episodes of uplift/subsidence (Fig. 1.3). It accords neatly with the plate tectonic interregnum labelled "global plate reorganization" in Fig. 1.3. The predicted increase in aridity (McGowran, 1979a) received some support from the discovery that grasslands may have emerged in the continental interior at that time (Truswell & Harris, 1982).

In the later Middle Eocene, the "new" global tectonic regime was established (Fig. 1.3) and its advent marked by the tectono-eustatic Khirthar Transgression in the Indo-West Pacific region (Nagappa, 1959; McGowran, 1977). That event is entered in Fig. 1.2 as an antidote to the prevailing view that Tertiary climatic deterioration is progressive, if episodic. In-

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stead, the importance of climatic reversals during the downward slide is stressed. The two most important reversals were in the later Eocene and the Early-To-Middle Miocene. Late Eocene sediments are more widespread on the continental margins and at numerous places on the platform than are any records since the Aptian-Albian. The palaeobotanical record is more widespread than for any other part of the Late Cretaceous or the Tertiary and the following statement by Truswell & Harris (1982) applies mostly to the later Eocene: "The widest coverage is provided by sites of Eocene age, and these suggest that rainforest grew through a wide area of central and southern Australia, across into the southwest and up into the northwest of Western Australia". The best known later Middle Eocene macrofossil floral assemblage occurs in the North Maslin Sands, south of Adelaide. It has been interpreted, on the basis of its epiphyllous fungi and its leaf physiognomy, as recording subtropical to tropical rainforest at $\approx 55^{\circ}\text{S}$ palaeolatitude (Lange, 1982; Christophel, 1981). The Late Eocene Golden Grove assemblage, also near Adelaide, records perhaps even warmer conditions (Lange, 1982). That is not inconsistent with the aspect of the Anglesea macro-flora (Christophel, 1981) in the southeast or the Werillup palynoflora (Hos, 1975) in the southwest of the continent. The marine record in southern Australia consists essentially of four successive transgressions, during which neritic marine carbonates were deposited for the first time since the Palaeozoic (McGowran, in press). Benthonic, tropical-type "larger" foraminifera, which had colonized the northern continental margin during the Maastrichtian and the Paleocene, migrated southwards during the later Eocene. This was not only due to the warming and climatic amelioration, but because southern Indian Ocean waters could deflect to the south of Australia for the first time, making it easier for excursions out of the tropics against counterclockwise gyres.

Finally, rapid increase in Australia/Antarctica separation began during the later Eocene, the last chance for marsupials to reach Australia (if that is what happened; perhaps they departed in the Cretaceous...).

Terminal Eocene Event and Oligocene Lacuna

A major step in the making of the modern ocean, conventional wisdom now has it, was the filling of the ocean basins with cold water (the psychrosphere). The "greenhouse" state, with salinity-dominated oceanic circulation, finally gave way to the "icehouse state" with temperature-dominated circulation. In the recent flurry of activity investigating the proposal that mass extinctions were extra-terrestrially induced catastrophes, there has been renewed scrutiny of what is known as the Terminal Eocene Event. It has long been known that there were major changes in the terrestrial floras and mammalian faunas in the north and that certain prominent "larger" foraminifera and planktonic foraminifera disappeared at the end of the Eocene. Changes in the biosphere clearly occurred over a several-million-year span, starting perhaps at about 40 mybp. Such changes are seen in foraminifera and deep ocean ostracods (Corliss, 1981; Benson *et al.*, 1984), in the plankton (Corliss *et al.*, 1984) and in neritic foraminifera in southern Australia (McGowran & Beecroft, 1986). Such changes commonly are interpreted in terms of changing palaeoclimatic and palaeoceanographic conditions, meaning, more specifically, a progressively deteriorating climate. Whilst the changing conditions are well documented, whether that deterioration was progressive is unclear; thus, the Late Eocene warm reversal after the Middle Eocene deterioration, as discussed above. There is also a modest cluster of marine extinctions at ≈ 36.5 to 37.0 mybp, just after the last extratropical excursion by Eocene tropical-type foraminifera

and at the point where oxygen-isotopic profiles show a sharp shift toward heavier values. The isotopic shift at the upper of the two "terminal" Eocene Events (Fig. 1.2) is interpreted as a sharp cooling (whether the last event in a trend or not). Alternative scenarios must be acknowledged, however, to account for the overall isotopic shift toward heavy oxygen from the Early Eocene to the early oligocene. The shift may have been due to temperature with an insignificant ice effect or increased salinity as icecaps grew. The latter view (Matthews, 1984) has been adequately answered by Shackleton (1984) and by Lloyd (1984).

The marine record is fairly complete on the South Australian margin and poorly developed elsewhere. The marine palaeontological record clearly indicates cool conditions, both in the absence of those warm-water forms that came south in the Eocene and Miocene and in the presence of the planktonic foraminiferan *Guembelitria* related to cool pulses (McGowran & Beecroft, 1985). The palaeobotanical record is restricted to the southeast coastal basins since, speculatively (Truswell & Harris, 1982) but almost certainly, aridity spread widely across the continent. Where it was wet, the floras were less diverse and of cooler aspect than in the Late Eocene (Kemp, 1978; 1981; Truswell & Harris, 1982). The Oligocene falls between major pulses of uplift/subsidence and volcanism in eastern Australia (Jones & Veevers, 1982).

The Miocene Oscillation

Australia's northward drift brought it into contact with island arcs of the southwest Pacific. A lower limit on dates for the intermingling of terrestrial biotas due to such physical contact may be Early Miocene (metamorphic dates entered in Fig. 1.3 as "arc collision II"). McGowran (1979b) summarizes the subsequent tectonic development of the island of New Guinea in the following broad-brush fashion:

- (i) the beginning of the Neogene: development of Aure Trough with volcanogenic source of sediments; onset of Sequence Three;
- (ii) the climax of the Neogene: intense Middle Miocene tectonism with maximum plutonism and volcanism in the Middle Miocene (Page, 1976), last extensive neritic carbonates;
- (iii) the Late Miocene interregnum; a time of plate tectonic readjustment to the foregoing; the actual geological record, pinned down by dates, is very poor and there seems to be extensive hiatus;
- (iv) the morphotectonic phase of Sequence Four: shallow water Middle Miocene limestones in several parts of the southwestern Pacific are overlain by bathyal Pliocene, itself now at almost two kilometres above sea-level. Spectacular fluctuations occurred in the past five million years. Veevers (1984) cites estimates of more than 600 metres per million years differential vertical uplift (northern New Guinea) and 2,000 meters per million years (Timor): "In terms of vertical motion, the northern margin today is lively, and the rest of Australia moribund".

The important point here is chronological parallelism. The later Early to Middle Miocene "climax" is the time of maximum transgression over Australia's margins. It is the time of a first order cycle of uplift in the southeastern Highlands and subsidence in the Otway and Murray Basins (Veevers, 1984). It is the time of renewed sedimentation in the interior. The Miocene land mammal faunal assemblages are concentrated in the interval spanned by the Batesfordian, Balcombian and Bairnsdalian Stages, that is the late Early to Middle Miocene (Woodburne *et al.*, 1985). Available palynological data are concentrated into the same interval (Truswell & Harris,

	TECTONISM	SEA LEVEL	CLIMATE	BIOTA	RECORD	DURICRUST	IN TERTIARY	
MODE ONE	rapid seafloor spreading	amplified: uplift, subsidence, igneous activity, CO ₂ exhalation	marine transgression	maritime climate, global warming, more humid, more equable	increased: habitat diversity, biotic diversity, evolutionary overturn	increased chance of sedimentary accumulation and fossilization (marine and nonmarine)	laterite and deep weathering	Middle to Early Miocene — — — Late to late Middle Eocene — — — Early Eocene to Late Paleocene
	slow seafloor spreading	subdued: uplift, subsidence, igneous activity, CO ₂ exhalation	marine regression	continental climate, global cooling, more arid, less equable	decreased: habitat diversity, biotic diversity, evolutionary overturn	decreased chance of sedimentary accumulation and fossilization (marine and nonmarine)	silcrete	Late Miocene — — — Oligocene — — — early Middle Eocene — — — Early Paleocene — — —

Table 1.1 A simplistic two-mode model of the conditions under which exogenic and endogenic processes could be predicted to occur. Changes between modes would be rapid and episodic.

1982) for the same reasons, namely that the climate was again warm and moist over substantial parts of the continent, including the interior.

The Miocene climatic reversal after the cold Oligocene is not a local Australian effect. The warm spikes in the high latitude profile (Fig. 1.4) can be matched with bipolar fossil evidence for warming (McGowran, 1979a; b; Fig. 38 in Veevers, 1984). Precisely as in Australia, the "late part of the early Miocene and the early part of the Middle Miocene has generally been regarded as the warmest interval of the Neogene" (Wolfe & Poore, 1982).

The geological record of the Middle Miocene is more extensive and more convincingly dated in all facies, marine and non-marine, than is the record of the Late Miocene. Whereas deep weathering is well established in the Early-Middle Miocene, the Late Miocene seems to be a time of silcrete formation (McGowran, 1979a). The globally well-established Late Miocene cooling and drying is reflected in Australia to a large extent by the absence of a record to the contrary. The coherent story that is emerging (Bowler, 1982), however, leads into the late Neogene, including Quaternary, history that is outlined below by Bowler.

GENERAL DISCUSSION

The theme of this account can be subsumed under: parallelism in tectonism and stratigraphic configuration; overall climatic deterioration with rapid episodic changes and pronounced reversals. The interesting and important changes are global and bipolar, not merely Australian. Table 1.1 sets out, baldly and simplistically, two "modes" in which it is possible to proceed from endogenic to exogenic phenomena such as surficial weathering and organic evolution. Because there are numerous feedbacks, changes will be threshold effects and will be rapid and episodic. Table 1.1, however, should be taken as a challenge. Is chemical weathering really so simple? Will organic evolution, as especially shown by

speciation and extinction rates, turn out to be neatly episodic? General points which need to be made are presented below.

(i) Chronological Resolution; Preservation of Fossils

These are the two great distorters of the record. Palaeobotanists, rightly, have taken care to acknowledge that the record is biased toward times of increased humidity, sedimentary accumulation and preservation of organic material (that is, some protection against oxidation). Regime One (Table 1.1) is better resolved and correlated than Regime Two, partly for the above and partly because increased evolutionary overturn delivers more biostratigraphic events. One must always weigh time against space when considering biogeographic-type or ecologic-type statements. Several authors, for example, have pointed to variation among Eocene rainforest-type floras (e.g. Christophel, 1981; Lange, 1982; Truswell & Harris, 1982). Three of the floras considered by Christophel (Golden Grove, Nerriga, North Maslin) may be spaced through some 15 million years. Geographic variation may be due to slight offsets in age in a time of rapid change.

(ii) Climatic/Environmental Changes Were Rapid and Transcontinental

This assertion underlies much of the present account. The so-called "larger" foraminifera, rich in symbiotic algae in shallow, warm seas, have a Tertiary record in the Indo-Pacific region in which fluctuations in their excursion polewards are well known. Taking the record at face value, with some hopeful correlations, Fig. 1.4 (from McGowran, in press) presents a theory of space-time distribution which emphasizes rapid, bipolar excursions in clusters that correlate with Sequences I-IV, respectively, (Fig. 1.3) and with "Mode One" in Table 1.1.

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The kind of climatic change that one would infer from the model in Fig. 1.4 bears on duricrust formation in Australia, an important background factor in Australian biohistory. Figure 1.3 and Table 1.1 imply an alternation of laterite and silcrete as a response to sweeping climatic change. That theory, based on some evidence of age and succession (McGowran, 1979a), survives in a state of benign neglect. The theory could be developed as follows: as aridity increased in three successive main episodes of cooling through the Tertiary ("Tertiary cooling I to III" in Fig. 1.3), so might silcrete formation increase as lateritization decreases in overall intensity.

The speed and extent of climatic change bear also on the tempo of evolution. For example, the question of whether rates of speciation respond statistically to environmental change could be tested, in the first instance, against climate. Again, the theory that marine mass extinction is more a result of climatic change than of anything else, including eustatic change and extra-terrestrial catastrophe (Stanley, 1984), can be tested. A scrutiny of the Terminal Eocene Event at ≈ 54 to 57°S shows a strong relationship between incoming species and transgression, on the one hand, and outgoing species (?extinction) and regression, on the other (McGowran & Beecroft, 1986), which does not accord with Stanley's model. Stanley, however, anticipated this by suggesting that tropical biotas are more vulnerable than are those at temperate latitudes. On land, it is expected that climatically transformed vegetation (from closed forest to a mosaic of grassland and woodland as in the Late Miocene of all continents) not only will fragment geographically the previous vertebrate faunas, but will place them under new and severe selection pressures that should be reflected in migration and speciation (Vrba, 1984).

(iii) Australia's Northward Drift Has Been Over-emphasized

In palaeobotany and geomorphology in particular, continental drift has dominated thinking. For students of marine organisms, especially of skeletonized protists in the benthos and in the plankton, the very strong parallelism of Australian climatic change with change in the rest of the world perhaps has been more continuously apparent. For Nix (1982), the palaeobotanical evidence for tropical/subtropical conditions in southern Australia in the early Tertiary can in fact be accommodated by annual mean temperatures of no more than 2 to 4°C warmer than present. Moreover, the northwards rafting of Australia has compensated for the general global cooling in the Tertiary. Nix presents a remarkably stable model of microthermic, mesothermic and megathermic belts across Australia through time. Much more in accord with the steps and reversals discussed here is the notion that, in the development of late Cainozoic aridity, "the relatively slow movement of continental plates was subordinate to major change in global circulation and that Australia was overtaken from the south by intensified subtropical high pressure belts migrating equatorwards" (Bowler, 1982). Over the Cainozoic as a whole, the (undeniable) drift is masked by the much more rapid global episodic tectonism and climatic fluctuation.

LATE CAINOZOIC ENVIRONMENT

Several features emerge in the above account as exerting a dominant control on past evolution and present environment of the Australian continent:

1. the long-term influence of our Gondwana connections;
2. the northward drift from Antarctica with the opening

of the Southern Ocean;

3. the tectonic style with a large stable platform or core of very ancient rocks against which eastern Australia, representing a formerly mobile belt (the Eastern Highlands), is now welded;
4. the presently active mobile zone of Papua New Guinea, the collision zone on the northern edge of the drifting plate;
5. the main area of continental Australia, now acting as a stable trailing platform isolated geologically and biologically (even nationally) by the presence of Torres Strait and the Gulf of Carpentaria from what is geologically the active region of the continental structure, namely the New Guinea Highlands.

In this way, the part of the drifting plate now identified as the Australian continent may be considered as a large stable system slowly drifting northwards. In this context, two elements combine to exert a dominating influence on environmental evolution: the long-term stability of the region and the climatic setting with zonal influence of the northern tropics, the mid-continental dry desert belt and the southern temperate winter rainfall region.

The implications of these factors, past and present, on the development of present landscapes, sediments and soils are examined in this section.

Tectonic Style

Of all the landmasses on the planet, Australia is often described as the oldest. Although partly a popular misconception, there is a sense in which it is true. Rocks of great antiquity are to be found in the core regions of each of the large continents on earth. The oldest Australian rocks of the Pilbara region (more than 3,000 million years old) have analogues of almost equivalent age in Canada and Africa. In another sense, however, claims for the unique aspects of Australian landscape antiquity are justified.

Largely, the age of the present landscape features makes the Australian setting special. The range of landscape expressions from the Kimberley and Arnhem Land Plateau in the north through the desert regions to the Flinders Range, Nullarbor Plain and southeastern highlands, across this whole transect the expression of landforms, sediments and soils, constitutes an array of unusual antiquity. Undisturbed by episodes of mountain-building or active volcanoes and lying within the climatic zone of high temperatures and strong weathering, these features result in a combination of environments unique on the face of the planet.

The Australian landmass, lacking active mountain belts, does not have the dramatic expression of the basin-and-range topography of North or South America nor the alpine features of Europe, India or China. Similarly, it lacks any comparable expression of the great rift systems with volcanoes and great lakes that have sundered the African continent. Instead, we see a land that preserves elements of landscape that existed 300 mybp, a land in which the rocks, exposed for so long at the surface, have worn down to low hills and ranges and are now so subdued that the erosion processes hardly have any effect.

Not only are the forms reduced to low relief, but the uppermost skin, the life-giving layer on which soils develop and on which plants and animals are totally dependent, has itself been affected dramatically. In this land of low relief, weathering rates are relatively fast and erosion rates slow. The overall effect is the production of deeply weathered soils from which the nutrients, particularly potassium, phosphorus and nitrogen, have been removed by millions of years of leaching

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(Northcote, 1986). In this context, the widespread occurrence of laterites and silcretes across northern and central Australia is the result of millions of years of weathering. Similarly, the extensive occurrence of highly calcareous soils or calcretes represents, in a sense, the next stage in the mobilization series.

Within this slowly eroding landmass, uplift along the eastern margin, the precursor of the present-day eastern highlands, maintained a general pattern of westerly flowing streams. During periods of high rainfall, when inland lakes were filled, these streams distributed large quantities of alluvial sediment over their interior floodplains. As long as the climate remained relatively humid, these deposits remained stable. With later onset of aridity, however, they provided the source of the extensive sandsheets and dunefields that now characterize interior Australia (Wasson, 1983). In this way, even the smallest drainage systems eroding catchment bedrock provided a continuous source of sediments to the alluvial inland plains, sediments which in the later phase of instability were extensively remobilized to form many of the aeolian features, especially dunes visible today.

The stability of the Australia continent provides one additional aspect that sets this land apart from most others. It enables elements of earlier environments to be preserved for very long periods. This aspect of longevity may be highlighted by considering the preservation of ancient drainage systems.

In the southwest of Western Australia, a system of interconnected valleys rises near the southern coastline and heads north inland before linking with the present course of the Swan River. This valley system, now dry and occupied by chains of salt lakes, represents the abandoned remnants of a system that once had its headwaters on the Antarctic continent when the two landmasses were linked. At the time of separation of the Australian Plate from Antarctica, the drainage system was beheaded; the now abandoned valleys remain as mute testimony to those ancient times.

In terms of their age, these pre-rift valleys certainly are older than 65 million years and, indeed, may date back to as much as 100 mybp, making them amongst the oldest drainage features anywhere on earth.

Similarly, many of the extensive salt lake systems on the northern margin of the Nullarbor Plain lie in the abandoned tracts of what were once large rivers flowing into the Tertiary sea. Today, they have been filled, largely by clays within which the salt lakes have formed. The ancient valleys represent legacies of humid climates of middle to lower Tertiary age in a landscape where surface water rarely flows today.

The ability of the Australian continent to preserve ancient features extends to the latter part of the time scale enabling us to identify rivers, lakes and dunes which, in other continents with more active depositional systems, would be obliterated by erosion or buried beneath thick covers of younger sediments.

Evolution of Eastern Highlands

The Great Dividing Range (great only in length rather than height) forms one of the principle landscape features controlling drainage and sedimentation over large areas of eastern Australia (Ollier, 1978). Its origins formerly were related to relatively recent geological events associated with what was known as the Kosciusko Uplift. Research in recent years, however, has established that the general elements of relief certainly were present 20 million years ago and probably much earlier (Wellman, 1979; Lambeck & Stephenson, 1986). Within that time, there has been only slight increase in elevation, with streams down-cutting through basal flows

emplaced in earlier valleys whose floors were cut deeply onto a landscape already uplifted to near present elevation (Jones & Veevers, 1982; Brown, 1983). Near Cooma, the present Murrumbidgee River has only just cut below the base of the ancient lava-filled valley.

This area of Australia's greatest relief has a relatively long and stable history by comparison with mountain ranges in other parts of the world. In this context, slopes and drainage basins have had a long time to adjust to the elements of time and relief. This results in mature, rounded topographic outlines associated with deep, broad valleys with gentle slopes. The headwaters of the major rivers of the Murray-Darling drainage basins reflect this long period of evolution in their catchments. The result is generally low energy streams carrying largely fine grained sediment which wend their way sluggishly across the flat inland plains to the sea. In this way, the evolution of the highlands exerts an important influence on the streams and drainage basins which draw waters and sediments from that source, an influence that we now know existed throughout most of the Tertiary.

Continental Interior – Tectonic versus Climatic Influence

The special setting of the Australian continent provides an opportunity to examine the relative influence of climate and tectonics on landscape evolution, an opportunity that is perhaps unique anywhere on the globe. Two basic principles are the starting point for our consideration.

Because the continent once lay further south, the environments formed at that time reflect the controlling climates of those regions. Analysis of the ancient evidence helps reconstruct those conditions (Bowler, 1982).

The implications of drift from higher to lower latitudes are such that, while temperatures are likely to increase, there may be a corresponding increase in tropical humidity.

In what way do these events relate to present-day arid features?

In recent geological history, the continent preserves evidence of major changes in climates and hydrological regimes. Some of these changes can be related to the equatorward drift with progressive increase in tropical influences, but that is far from the full story.

In Miocene times, huge inland lakes existed where only desert dunes occur today. Moreover, when the Lake Eyre and Lake Frome basins contained permanent freshwater bodies, they were associated with plants and animals including crocodiles and flamingos, which we more characteristically associate with warm, humid environments. At the same time, basins in southeastern Australia were the locations of huge swamp forests, the precursors of the brown coals of the Latrobe Valley and Bacchus Marsh in Victoria. Rainforest vegetation extended throughout large regions of the Murray Basin. Eucalypt forests, if present, were restricted to small pockets only. This situation was associated with deep weathering, producing lateritic soils.

Across the southern margins of the continent, the low-lying areas such as the Nullarbor Plain, the Murray Basin inland to Kerang, the Port Phillip and Otway Basins and East Gippsland were all invaded by the sea. Extensive deposits of shelly limestone date from this period.

By 10 million years ago, the system had begun to change. Growth of ice in Antarctica was locking up water from the oceans causing sea-levels to fall progressively. This occurred slowly at first, until about 6.6 mybp ago when the oceanic and continental evidence suggest a relatively rapid reduction in levels. At that time, the sea retreated from a substantial

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portion of southern Australia, leaving large areas of the Murray Basin, the Nullarbor Plain and other regions previously submerged, as dry land. A whole new set of conditions was initiated across southern Australia. The scene was being set for the later development of the modern Australian landscape.

If the period before 6.6 mybp was relatively wet across most of the continent, it stands in marked contrast to the dry, arid environments of today. The rainforests of the inland region have long since given way to arid-adapted eucalypt and acacia woodland. The large calcareous lakes of the Eyre-Frome region have dried, leaving a legacy of small playas or mudflats where evaporating saline waters now deposit gypsum crystals. The siliceous and lateritic soils of ancient times have been replaced by calcareous and gypseous profiles. This dramatic change constitutes something of a milestone in the development of the whole physical and biological setting and warrants further attention.

Stretching across inland and southern Australia, the contrast between pre-Pliocene environments, with acid weathering profiles and the overlying alkaline sediments, and younger soils provides a key to the nature of the change from humid to arid regimes. The paradox of Australia's arid climate is striking. Although 20 mybp the continent lay some 1,200 km or 10° of latitude further south in what are much colder regions, the evidence of the plants and animals of that time, as indicated above, suggests environments that were actually warmer and certainly wetter than experienced by the same basins in their lower latitudes of today. If the present climatic zones (tropics, mid-latitude dry belt and southern temperate winter rainfall belt) had been in their present form in the Miocene, then the regions of northern Australia, near Arnhem Land and Cape York, would have straddled the mid-latitude dry belt. This would have been the location of Miocene deserts if such had existed at that time. As the continent drifted north, deserts would have expanded progressively towards the south. On the northern side, dunes, evaporite sequences and other expressions of aridity would have been carried further into the tropics. The legacy of such events, however, is not preserved. On the contrary, the present evidence suggests that during the Miocene, the present dry mid-latitude belts that today form the dominant control of the world's major deserts (including central Australia), did not exist in their present form. In fact, events associated with the growth of the Antarctic ice cap, the opening of the Southern Ocean and subsequent cooling of the warm Miocene seas probably changed the nature of zonal or atmospheric circulation. In the Miocene, the influence of relatively warm ocean temperatures maintained humid conditions across the continent.

With the relatively sudden cooling of sea surface temperatures near the end of the Miocene, atmospheric pressure systems were intensified and circulation was accelerated. In the mid-latitudes, a most important consequence of these changes was the amplification of the blocking high pressure systems that effectively inhibit incursions of maritime air masses into the continental interior. In this way, conditions controlling the dry desert regions of the globe were initiated or intensified.

Before these dramatic changes, the Australian climate was characterised by low seasonal contrast; warm wet summers alternated with cool, humid winters. Such conditions favoured the development of deep, acidic weathering profiles typical of that time. After the retreat of Tertiary seas, cooling of the oceans and disappearance of inland freshwater lakes with their associated rainforests and warmth-loving animals, the seasonal contrast increased. Summer rainfall diminished, giving rise to seasonal hydrologic stress. At the same time, wind velocities increased and the conditions were initiated that gave rise to those prevailing today.

Plio-Pleistocene Transition

For some three million years after the retreat of the sea, the landscape and its biota were in a transitional phase between the humid- and arid-adapted forms. During this interval, the climate was, at times, wet enough for some deep and acidic soils to form across southern Australia. One of these, known as the Karoonda Surface (Firman, 1973), involving a thick iron and silica cemented horizon, can be traced from inland near Lake Frome across the Murray Basin in the southeast. Throughout large regions of southern and inland Australia, the iron-cemented, acidic and often deeply weathered profiles of Pliocene age are often abruptly overlain by alkaline, calcareous sediments and soils. The contrast is most striking. Often the uppermost layers cannot be derived simply by weathering of the materials on which they rest. The only way these fine-grained sediments and soils can be explained is by wind transport. Thus, an entirely new element became apparent in the landscape: the development of predominantly alkaline soils and extensive aeolian deposits.

Although the first appearance of those conditions that mark the amplification of aeolian processes is hard to identify, the onset of the dominantly alkaline weathering phase is placed near 2.5 mybp.

Since that time, dry windy conditions periodically have resculptured the dunes and deflation basins of the interior, processes typical of the Quaternary Period in this region.

Ice Ages and Deserts – The Quaternary Record

The Quaternary, the most recent and shortest of the major geological time divisions and a period of Ice Ages, represents an extraordinary episode in earth history. Not since the Permian, some 250 million years earlier, did the earth experience such an expansion of cold climates as those which characterize Quaternary environments.

The origins of these dramatic changes that have left their imprint on both the physical and biological elements of this continent lie in the complex sequence of earlier events, some of the most important of which are found in the southern regions of the globe. They include the opening of the Southern Ocean, the increased elevation by uplift along alpine belts especially in the Himalayan-Tibet regions, the growth of ice in Antarctica and eventual cooling of global oceans. These elements set the scene for that period of drastic geological change associated with the age of ice. Additionally, this period was the time of human evolution, radiation and migration. As such, it has immense biological implications.

The cold climate processes had developed sufficiently 2.5 mybp to set up the geologically new conditions. These developed with cyclic repetition of cold (glacial) and warmer (interglacial) periods alternating about every 100,000 years. Throughout the past two million years there may have been some 19 cycles in which cold and warmer conditions have alternated, at the same time producing major changes in water balance throughout the land. In this context, there is no constant relationship between temperature and water availability. The periods of warmer or intermediate temperature change were wetter than the coldest intervals. The exact way these multi-cyclic events affected the landscape, especially in the earlier Quaternary stages, remains to be clarified. Our understanding is based largely on events of the last glacial-interglacial cycle that began about 120,000 and ended as recently as only 10,000 years ago.

The Last Glacial Cycle

The last glacial cycle began 120,000 years ago with environments that resembled those of today. Shore lines and sea-levels were close to present configurations (Chappell, 1983). Inland Australia was dry, with stabilized dunes standing as reminders of previous arid, dune-building environments. At first, the changes were slow and relatively minor. The progressive build-up of ice in the Northern Hemisphere continents hardly had any influence in Australia until about 60,000 years ago, when run-off increased in the rivers draining the southeastern highlands. Thus, the Murray, Murrumbidgee and other rivers draining into the Murray Basin contributed to the flooding of previously dry lake basins there and a regional rise in watertables (Bowler, 1978). In the Willandra Lakes, fed by a tributary of the Lachlan system, more than 1,000 km² of permanent lakes were maintained and even overflowed into the Murray. This period persisted until 36,000 years ago when a short-lived reversal in hydrologic balance temporarily dried the lakes and produced a phase of dune-building (Bowler & Wasson, 1983). The wet conditions, however, returned and persisted until about 25,000 years ago when the system began to change towards drier environments as the progressive onset of cold conditions approached maximum expression in the catchments.

With the advance towards the glacial maximum, snow lines descended as much as 1,000 m below present elevations. Wherever elements of the landscape rose above the depressed snowline, these provided favourable sites for ice accumulation and the development of glaciers or ice caps. In Australia, the snowline depression was sufficient only to bring the summit levels of a small region near Kosciusko on the mainland and the West Coast Range and Central Plateau of Tasmania under the influence of glacial processes. Beginning about 30,000 years ago, these environments developed until the stage of maximum cold with largest development of ice was reached about 20,000 years ago, leaving a legacy of characteristic landforms and sediments.

Although areas directly affected by glacial ice were small, limited to the highest and most southerly regions, a much larger area came under the influence of periglacial phenomena, in which freeze-thaw seasonal oscillations play such an important part. These processes were capable of mobilizing soil layers, producing slope instability, building fans on lower slopes and contributing large quantities of sediment into upland stream catchments and channels.

During the maximum of the last glacial period, about 20,000 years ago, many of the scree slopes of southeastern Australia and Tasmania were re-shaped with a young mantle of frost-shattered debris deposited and carried to lower levels. On termination of the cold conditions, these mantles were stabilized and, with the return of woodland vegetation to previously treeless slopes, soil development has proceeded to the present day.

Aridity and Inland Australia

The processes that produced the cold climates had a profound influence on the hydrology, wind systems and seasonality across the entire continent. Reductions in global temperatures, especially the cooling of the oceans and lowered evaporation rates, reduced the availability of atmospheric moisture, leading to a decrease in available precipitation over large regions (Bowler & Wasson, 1983). In places such as the headwaters of streams draining periglacially affected catchments, this change was largely off-set by increased run-off in montane streams, but on the distant plains of the inland, the effects were more drastic.

Assisted by high velocity winds associated with intensified pressure systems, periods of hydrologic stress comparable to long and frequent droughts became the pattern of the time. Coming after a period of water abundance during which many inland basins, dry today, were converted to permanent water-bodies, the period of aridity had a profound influence on plants, animals and human occupants. Even in Tasmania, lakes in the centre and southeast of the island dried out; dunes and sand sheets extended across neighbouring plains.

Across southern and inland Australia, sand dunes constructed during early glacial episodes were reactivated and new ones were formed. Large fields of dunes advanced eastwards across the Murray Basin, forming the fields known as Big Desert and Little Desert; the longitudinal dunes of the Simpson and Strzelecki Deserts were extended.

Although longitudinal dunes are most characteristic of the Australian sand deserts, they are often associated with, indeed many originated from, transverse dunes formed on the downwind side of rivers and lakes. Of particular relevance are the clay-rich dunes or lunettes, those crescentic-shaped dunes formed on the eastern side of lake basins across southern Australia from the southwest of Western Australia to the Australian Capital Territory and Tasmania. These deposits often preserve faunal remains (such as Tandou and Menindee on the Darling River) and in some cases are rich in archaeological evidence. Extensive human relicts on the lakes in the Willandra system, especially Lake Mungo, represent some of the richest deposits of their kind in the world. These clay-rich dunes, which are often saline and contain gypsum and previously dissolved chloride, were built by wind erosion of drying lake floors.

These events occurred extensively across the continent near the peak of the last glacial period, when the earlier wet conditions gave way to extended aridity. Such environments of dune-building expanded northwards to near the Gulf of Carpentaria and southwards into eastern Victoria and Tasmania.

During this time, large quantities of dust and salt were transported downwind to be deposited as a mantle across the landscape. Even during severe droughts today, dust raised in interior Australia travels as far as New Zealand. These materials accumulated through time to form a red silty-clay layer known to pedologists as parna, the Australian equivalent of the loess deposits of Europe, America and China. Such materials extend across the Murray Basin to the hills of the southeast, in the path of ancient dust storms that accompanied the glacial aridity and erosion of large areas of the inland some 25,000 to 16,000 years ago. The regional implications of these environments, in terms of salt budgets and affects on soils and plants, remain to be evaluated more fully.

In northern Australia, although data are more spare, the available evidence suggests parallels between events identified in the southern, more temperate regions, although the actual timing may turn out to be slightly different from north to south.

By about 15,000 years ago, the severest glacial stresses were coming to an end. Five thousand years later as the ice retreated from global ice caps, returning melt waters produced a world-wide rise in sea-level. Tasmania's link with the mainland was severed with the flooding of Bass Strait, permanently isolating its flora, fauna and humans. The Gulf of Carpentaria was flooded at the same time, with important climatic implications for increasing rainfall over large adjacent areas of the Northern Territory and Queensland. In general, the harsh conditions that characterised environments of full-glacial age had given way by 10,000 years ago to conditions rather similar to those of today.

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The glacial age environments across continental Australia may be summarized:

1. during glacial winters, air masses from the ice-affected Southern Ocean penetrated deeply into the interior, intensifying cold frosty winter conditions;
2. spring winds, particularly northerlies and westerlies, greatly accelerated by amplified pressure systems, swept across the southern regions of the continent. The trade winds on the northern monsoonal regions were similarly accelerated. The strong winds, combined with the extended frost incidence, resulted in a much delayed growing season, compared with that of today;
3. the persistence of periglacial environments in the south-eastern highlands and Tasmania would have maintained high runoff, even though overall precipitation was reduced. Across inland Australia, subjected to radiation levels similar to those of today, evaporation loss enhanced by strong winds and reduced cloud cover actually may have been higher than at present. Strong winds, especially those associated with frontal systems, transported clays from saline depressions on lake floors, mobilized sands and constructed dunes across large areas of the inland.

These conditions of enhanced seasonality with cold winters and windier, drier summers associated with low sea-levels and exposed continental shelves, produced environments imimical to many plants. The eucalypt woodlands of the south, poorly adapted to frost and strong winds, were forced into protected pockets of the landscape leaving sediments and soils more exposed to the forces of erosion.

Holocene Environments – The Last 10,000 Years

Throughout the last 10,000 years, although significant changes have occurred in Australia's climate, these have been small by comparison with those of earlier glacial times.

Changes in water balance are expressed as changes of water-level in closed lakes in southeastern Australia. The volcanic crater lakes of Keilabete, Gnotuk and Bullenmerri in western Victoria record conditions between 8,000 to 6,000 years ago which seem to have been slightly wetter than today.

A relatively dry interval recorded between 3,000 to 2,000 years ago in the lake level data, finds equivalent expression in a phase of dune building in western New South Wales near Cobar (Wasson, 1976).

Conclusions

Australians live today in one of those interglacial periods which represent brief intervals of geological time. The climate we have inherited already has had a profound influence on the history of this continent's plants, animals and humans. Its modern expression affects almost every element of our daily lives.

The geological record demonstrates the reality of climatic sensitivity in which quite small variations in the earth's thermal budget can trigger off changes on a planetary scale sufficient to lead into or out of a complete Ice Age. The global reality of a world of rapidly industrializing nations, removing protective forests and discharging huge quantities of dust, smoke, carbon dioxide and other chemicals into the atmosphere represents a geological force new to the earth. The full implications of human influence on climate remain unknown and, therefore, of threatening dimensions.

The lessons of the past which are written indelibly on the face of the Australian continent permit an understanding of how climates have changed through time. In so doing, they provide a key to the future. Preservation of the physical and biological heritage depends on a deepened awareness of past events; to ignore them is to invite disaster.

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1. EVOLUTION OF AUSTRALIAN ENVIRONMENTS

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2. THE AUSTRALIAN MARINE ENVIRONMENT

J. S. BUNT

INTRODUCTION

No one of the Earth's seas exists as a body in isolation. Such compartmentation as does exist is imperfect and at best acts to impede or direct exchange between the parts. Thus, the Australian marine environment cannot be said to have seaward limits. To landward, its extent can be set with rather more confidence as the highest reach of the tides. Even there, however, precise limits are commonly difficult to establish in practice. Boundaries set by definition or legislation do not remove the essential uncertainty with which biologists, in particular, must live. In the treatment which follows, attention will be focused on the seas that touch or directly surround Australian shores. Emphasis will be placed on features and conditions which might be considered unique or peculiar to the Australian region. These arise primarily from geographic location, physical history and the manner in which those circumstances dictate the imposition of a variety of driving forces in space and time. Attention will be concentrated on the physical features and conditions of the present.

No comprehensive scientific account of the Australian marine environment yet exists. Several reviews cover particular topics or sub-regions and these have been used wherever possible as primary information sources. Even so, the level and type of detail available is highly variable and frequently inadequate.

This account begins with geographic considerations, proceeds to the physical substrate and only then to the fluid medium itself, beginning with its motions and exchanges and finally treating the physico-chemical properties of the milieu and, at the end, its nutrient resources. Only the most obvious and powerful influences exerted by living communities on environment are acknowledged.

The divisions of the marine environment adopted by Sverdrup *et al.* (1970) (Fig. 2.1) are used throughout the text. Concern is essentially with description rather than explanation. For underlying chemical and physical principles and for the theoretical treatment of mechanisms and processes, reference should be made to the more specialized literature. Topics such as physical oceanography are treated in a non-analytical fashion, in an attempt to convey the effects of physical processes, which are the first concern of the biologist.

THE GEOGRAPHIC BASE

Calculations indicate that continental Australia is moving northward at a rate of around 60 mm/year (Wilford, 1979). Accordingly, the land mass may be assumed to have been within one degree of its present latitudinal limits for some $1-2 \times 10^6$ years. Within that time frame, sea-levels, and hence the extent and disposition of the shoreward marine domain, have varied considerably. Modern sea-level is considered to have prevailed for some 6,000 years (Grindrod & Rhodes, 1984). The setting of the present Australian marine environment and its overall geographic stability may be viewed conveniently within those limits.

The environment considered is directly associated with two major and a number of minor land masses, of which the principal one, Australia, lies broadly between latitudes 10°40'S at Cape York and 43°39'S at South East Cape, Tasmania; and longitudes 112°59'E at Cape Inscription in the west and Cape Byron at 153°38'E in the east. In its position to the immediate north of Australia, the island of greater New Guinea is relevant in the tropics. The islands of Indonesia which sweep away from the northwest are relatively close by at their eastern limit. To the east-southeast, the North and South Islands of New Zealand are much further removed. Antarctica, to which Australia was once connected, now lies across some 2,500 km of open ocean to the south. The Indian subcontinent and Africa are neighbours only to the extent that they have coasts bordering the Indian Ocean. Other than to the north, then, Australia and its marine domain are isolated geographically.

Accordingly, the Australian benthic, if not oceanic or pelagic environments, may be reasonably well circumscribed between the coast and the boundary of the abyssal plain. The limits are indicated in Fig. 2.2 (based on Jones, 1979) and modified to indicate the approximate extent of the eulittoral and sublittoral zones as defined by Sverdrup *et al.* (1970). Together, those zones may be taken to correspond to the extent of the continental shelf. No attempt has been made to delimit the archibenthic and the abyssal benthic zones which lie beyond the continental shelf, largely because little or nothing biological is known of them for Australia.

Within the partially arbitrary limits of Fig. 2.2, the extent of the Australian continental shelf may be estimated at 2.5×10^6 km². Of that total, 52% is occupied by the eulittoral zone. The extent of the deep-sea benthic system to the margins of the abyssal plain is 3.3×10^6 km². Rather more detailed statistics within convenient geographic elements, as marked in Fig. 2.2, are presented in Table 2.1.

Within the eulittoral zone, Galloway (1981) has estimated that water bodies at the coastline cover a total area of around 8,250 km² made up of 4,300 km² of estuaries, 2,550

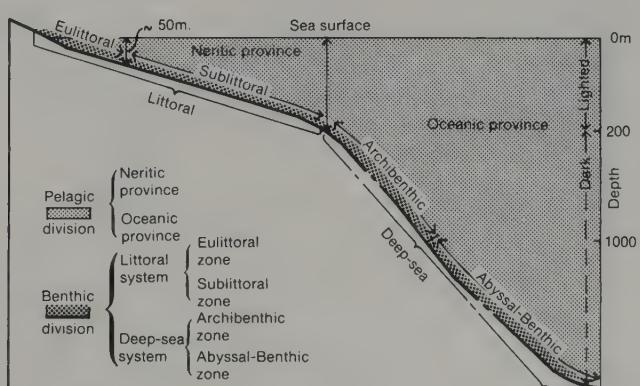


Figure 2.1 A system of terms for describing major divisions of the marine environment. (After Sverdrup *et al.*, 1970)

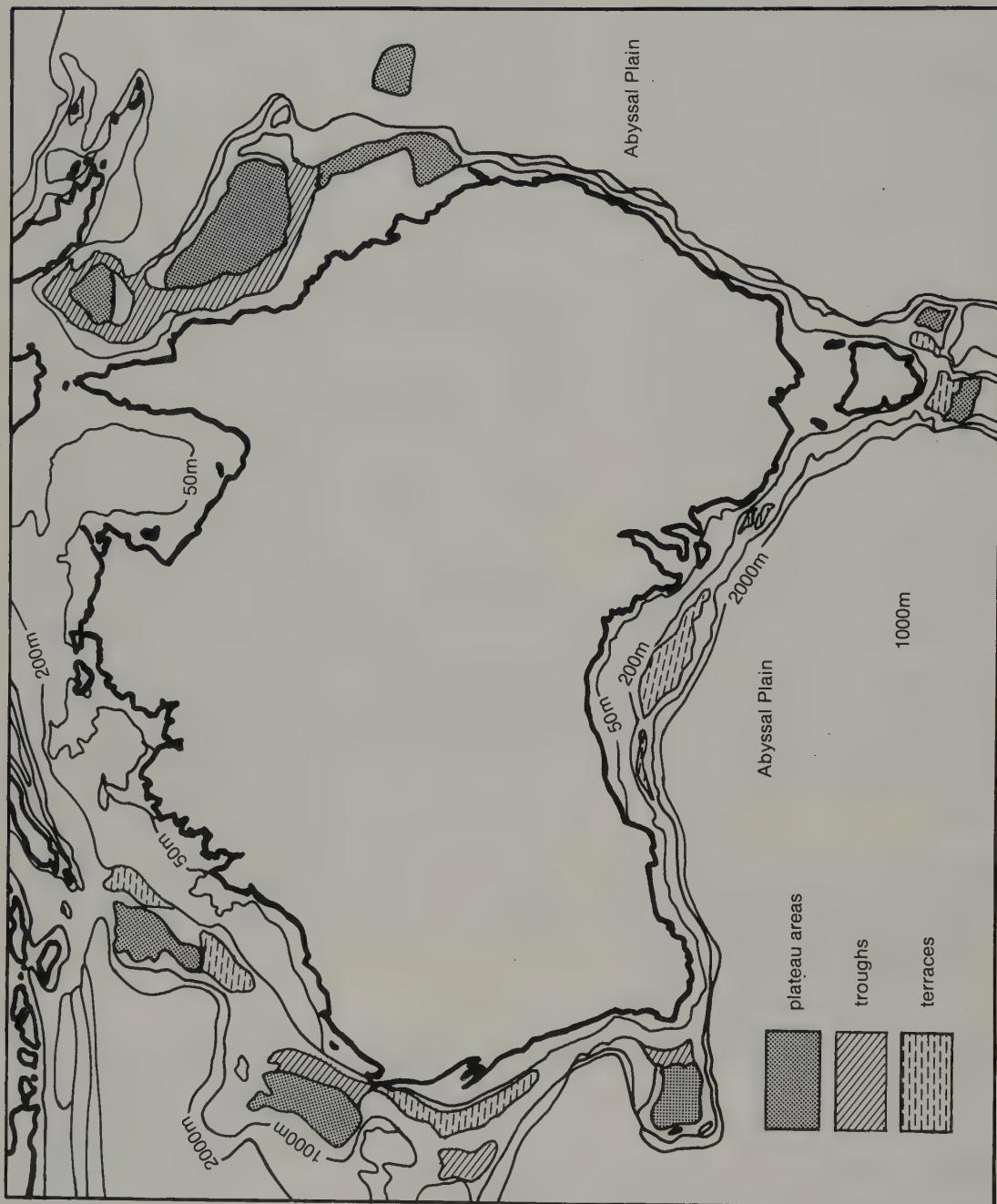


Figure 2.2 Major features of the benthic environment in the Australian region. (After Jones, 1979)

km^2 of inlets with entrances less than 1 km wide and 1,400 km^2 of tidally influenced lagoons. Intertidal surfaces are estimated to occupy a further 16,100 km^2 .

Finally, in respect of geography, some comment should be made on the length of the coastline. Considering this question, Galloway & Bahr (1979) confirm that such measurements are essentially indeterminate. Using intercepts of 0.1 km on 1 : 250,000 maps, however, and including all nearby islands greater than 12 ha in area, they obtained a measure of 69,630 km for Australian shores. This figure reduces to 30,270 km using 10 km intercepts (Galloway *et al.*, 1980), on which basis it is informative, if ecologically arbitrary, to list coastline lengths. By State, these are (in km): Queensland 6,080; New South Wales 1,740; Victoria 1,720; South Australia 3,270; Western Australia 10,100; Northern Territory 5,030; Tasmania 2,230.

For additional detail, especially relevant to the coast, the reader is referred to Galloway (1981), his colleagues and the computer data base they have established.

GEOLOGICAL SETTINGS

Introduction

The spaces, structures and substrates associated with the bed of the sea and its coastal margins are fundamental elements of the marine environment. Their present dispositions and character relate directly to the complex events of the geologic past and are subject to continual change which may range from undetectably slow to dramatically swift according to circumstance. Since this account is concerned with what now exists, essentially only the lower boundary of the aquatic province, and not with the originating mechanisms or substructures, no attempt will be made at reconstruction. For those seeking background on continental drift and associated events over long time scales, a useful short account has been prepared by Habicht (1979). A concise, contemporary account of the evolution of the Australian continental margin and its coasts may be found in Jenkin (1984). Greater detail on the same subject has been offered by Falvey & Mutter (1981). The 1979 Bureau of Mineral Resources *Earth Science Atlas of Australia* provides well-illustrated overview articles which extend to the marine domain and relate not only to continental drift but as well to crustal geology, sedimentary cycles, continental drainage and palaeogeography. Shepard (1963) offers a valuable reference text while a review by Plumb (1979) deals specifically with the tectonic evolution of Australia.

Physiography of the Shelf and Continental Margins

Generally, the scales and form of geological data available are only partially adequate to the needs of biologists and ecologists. Thus, for the most part, only relatively gross physiographic attributes of the seabed are documented. Rather more detailed information is available at the coasts although, even there, comprehensive descriptions tend to be limited to features of particular interest to the geologist.

The submarine physiography around continental Australia is dominated by a set of distinctive features, including the continental shelf, the continental slope and rise, and, along with those, various terraces, plateaus and troughs as well as canyons (Fig. 2.2). The abyssal plain, which extends into the ocean basins beyond the continental rise, is sometimes marked by seamounts or tablemounts.

Table 2.1 Plane areas of sea bed around Australia in several categories derived from Fig. 2.2.

PROVINCE	AREA (km^2)
From Coast to 50 m depth	1 298 000
From Coast to shelf	2 505 000
From Coast to Abyssal Edge	5 826 000
Terraces	249 000
Troughs	403 000
Plateaus	476 000
Slope	1 514 000

The continental shelf is continuous in extent, although it ranges from less than 15 km in width off southeastern coasts to greater than 400 km into the Timor Sea and extends between the coasts of New Guinea and Australia in the region of the Arafura Sea and Torres Strait. Its outer limit lies at depths around 150 m where there is generally a marked increase in gradient towards the top of the continental slope. The shelf proper is not necessarily featureless topographically. Fairbridge (1952) has recorded that the Sahul Shelf off northwestern Australia bears many features in common with the landward Kimberleys, an indication of comparatively recent inundation. Rather the same may be said of the shelf off northeastern Queensland, where the present Great Barrier Reef occupies the higher areas of past subaerial features. Indeed, the living reef has contributed materially to shelf topography. Canyon features extend into and across the shelf, particularly at locations off southern and southeastern coasts. On present evidence, however, these appear features of the slope rather than the shelf. Jenkin (1984) cites attention by other authors to a variety of submerged coastal features including beach rock, sand ridges, aeolianite dunes, terraces, ridges and cliffs. Clearly, departures from topographic monotony on the shelf are common, as attested by Shepard (1963).

Unlike the shelf, the continental slope is not fully continuous around Australia. Further, its extent is quite variable and it is commonly interrupted by other features. Worldwide, the gradient of the slope averages around 4°, but inclines of up to 40° are not uncommon around Australia, often leading without interruption to abyssal depths greater than 4,000 metres.

Within the slope, three major and several minor terraces as well as four major plateaus and several troughs exist off Western Australia. Four terraces occur off southern coasts. Troughs, plateaus and an associated trough are substantial features of the western Coral Sea within the Queensland continental slope. The Tasman Abyssal Plain and the Cato Trough effectively isolate the eastern margins of Australia from the Kenn Plateau, the Lord Howe Rise and associated physiographic elements a little further to the east.

In general, the plateaus referred to have their shallowest depths around 900 to 2,000 metres. Reasonably detailed accounts of the Western Australian continental margin are presented by Veevers (1974) and Powell (1982). Willcox (1978) and Connolly & Von Der Borch (1967) report data for the continental margin of the Great Australian Bight and Mutter & Karner (1980) describe the continental margin off northeastern Australia. The scale and nature of those studies make it difficult to establish whether and to what extent the plateaus and terraces of the region are topographically irregular. Studies by Falvey & Veevers (1974) demonstrate that the Scott and Exmouth Plateaus, at least, are topographically

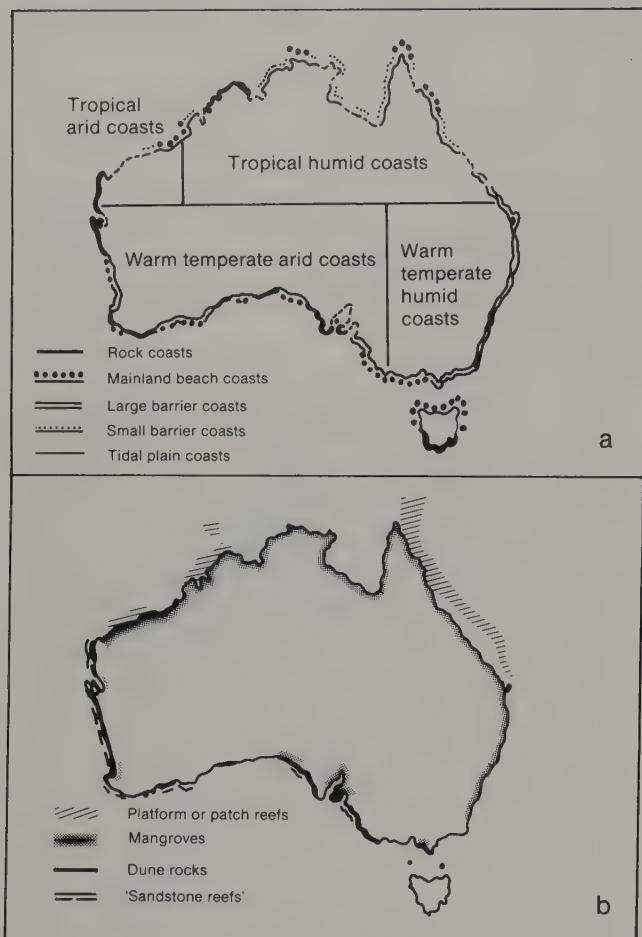


Figure 2.3 Coastal types around Australia. (After Davies, 1977)

complex. Further, both the Exmouth and Scott Plateaus are directly or indirectly associated with evidently prominent submarine canyons (Fig. 2.2).

Like the slope, the continental rise is variable in its development. In some places, notably off the eastern coast, the rise appears to be virtually absent. Beyond the rise, the abyssal plain to the east, west and south of the continent may be taken to be generally featureless, with the exception of the Tasmanid Sea Mounts roughly along 156°E, centred within the Tasman Abyssal Plain.

Geomorphological Features at the Coast and Nearshore

Largely because of relative ease of access, a great deal more may be said about the physical character of the land-sea interface than about the continental margin proper. For a continent the size of Australia, the subject of coastal and nearshore geomorphology is complex and, in many respects, unique. Its study is by no means complete and, not infrequently, still pioneering in nature. This account is based on those of Jennings & Bird (1967), Davies (1977) and Thom (1984) and colleagues, augmented by the substantial database of Galloway (1981). The reader may find useful a text by Bird (1976), a good deal of which relates to Australian conditions. The literature of geomorphology deals necessarily with formative processes, notably the influences of climate and sea on the development of landforms. The fact that those influences are pivotal will largely be taken for granted for the present so that the broader environmental significance of waves, tides, currents and so on may be considered in their own right in subsequent sections.

In treating the coast of Australia, it is necessary to recognize that, at the largest scales, coastal configuration reflects major geological processes of the past (Davies, 1977). These relate to origination of the Australian Plate, to subsequent rifting at the margins and to cycles of sedimentation in continental basins. The latter have been influenced by climate through time and by real or relative changes in sea-level. Some of the essential background for such scales are described by Jenkin (1984). Clearly, many of those relatively large features owe as much or more of their physical character to crustal processes of regional or local scale as to erosional and depositional phenomena. Spencer Gulf, for example, relates to two major geological provinces of late Precambrian age (Gostin *et al.*, 1984) and the origin of the Gulf of Carpentaria is considered to have been associated with block faulting in the Pleistocene (Fairbridge, 1966). Four basic coastal sectors can be recognized (Fig. 2.3), all distinguished in terms of process environments (Thom, 1984; Davies, 1977), not the underlying geological structures. Observe, nonetheless, that a topographic series has been identified in Fig. 2.3a as the coast becomes more low-lying and that additional elements have been added in Fig. 2.3b, *viz.*: reefal structures, dune rocks and mangroves. The latter, in that scheme, is merely an identifier of coastal type. Coral reefs, on the other hand, although biogenic, may be considered true geological structures. Gill's (1982) "eight coasts" are more broadly descriptive but nonetheless useful as shown in Fig. 2.4. Certain of the notable geomorphic features associated with each environment by Davies (1977) are as follows:

Warm Temperate Humid Coasts. The beaches of this region are a common, often dominant, coastal feature and range considerably in size from the quite small in southeastern Tasmania, to the more continuous in the northeast of the island and in western Victoria. Similarly, barrier beaches increase in size northward along the eastern coast of the mainland toward southern Queensland. Estuaries, another

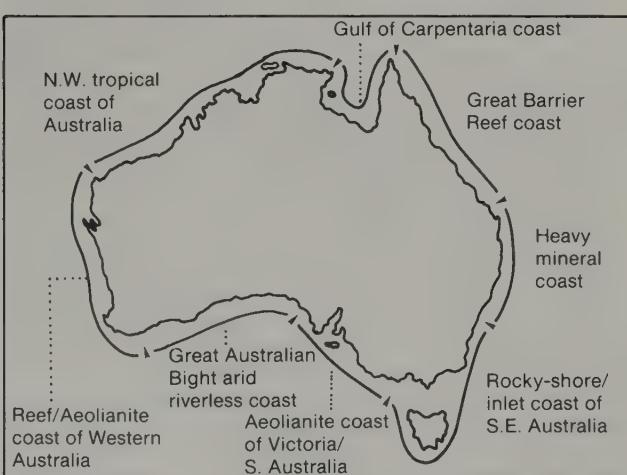


Figure 2.4 An alternate system of coastal types for Australia. (After Gill, 1982)

Table 2.2 Areas of major coastal land forms (km^2). Seasonally dry lake bed data not included.

LANDFORM	QLD	N.S.W.	VIC.	S.A.	W.A.	N.T.	TAS.	TOTAL
Dunes, beaches & beach ridge plains	5 109 18.8	1 236 16.3	1 653 28.0	5 613 53.4	12 057 33.4	1 242 5.5	984 13.8	27 897 23.8%
Low rock terrain	1 407 5.2	1 938 25.6	724 12.3	969 9.2	2 832 7.8	390 1.7	1 974 27.7	10 234 8.7%
High rocky terrain	2 198 8.1	1 365 18.0	432 7.3	279 2.7	5 142 14.2	552 2.4	2 247 31.5	12 215 10.4%
"Tertiary" terrain: mainly non aeolian sand & laterite	1 212 4.4	144 1.9	939 15.9	129 1.2	2 076 5.7	5 271 23.3	414 5.8	10 185 8.7%
Intertidal mud	4 527 16.6	117 1.5	150 2.5	459 4.4	5 643 15.6	5 742 25.4	33 0.5	16 671 14.2%
Supratidal mud	8 522	117	198	558	4 218	6 675	57	20 345
Alluvium	2 652	1 518	1 203	993	1 977	1 581	714	10 638
Water (estuaries etc)	1 596 5.9	1 128 14.9	597 10.1	1 503 14.3	2 187 6.0	1 146 5.2	705 9.9	8 862 7.6%
Total	27 223	7 563	5 896	10 503	36 132	22 599	7 128	117 044
Coasts with cliffs > 2m (km)	4 875	565	465	1 023	1 950	548	664	
Coast length	≈6 000	≈1 700	≈1 700	≈3 500	≈1 100	≈5 200	≈2 500	
% Cliff	≈8.0	≈33.0	≈27.0	≈29.0	≈18.0	≈10.0	≈27.0	

common feature, will be considered below. Davies (1977) observes that "this coastal segment is *par excellence* the home of the high tide shore platform".

Warm Temperate Arid Coasts. Broadly, this segment is marked by the rarity of estuaries and coastal inlets as well as of tidal plains. On the other hand, dune rocks with resultant cliffs and sandstone reefs are extensive. Notable are the Zuytdorp Cliffs towards the mouth of the Murchison River, which run a total length of around 130 km at heights between 100 and 200 metres. Where truncation has not occurred, as in Shark Bay, the shelter offered to those waters is marked.

Tropical Arid Coasts. This relatively short segment is characterized by beach fronts of low gradient and wide tidal plains. Massive beach rock is common. Offshore islands in some sectors add to shelter at the coast. Exmouth Gulf, a significant feature, is not included in Davies' (1977) treatment.

Tropical Humid Coasts. Davies (1977) accepts that his special concern with processes cannot override the considerable structural diversity in this segment of the coast. Even so, he makes the point that environmental influences, including cyclonic events, are so strong that fine sediment deposition is a major feature of the coastal landscape. Rocky shores tend to be intermittent except in the Kimberleys or where bauxite occurs at the shoreline. For the eastern seaboard, any generalizations concerning sedimentation should be viewed against the existence and influence of the Great Barrier Reef, itself a major structural feature. Fringing coral reefs, both on the coast adjacent to the Great Barrier Reef and elsewhere in the region have much more limited geomorphological significance, but are, of course, important indicators of environmental character.

Specific Categories of Coastal Feature

Beyond the characterization of coastal landforms and a recognition of the process environments with which they are linked, the physical structures associated with particular classes of landform must be considered if living environments are to be specified. For biological purposes, this requires information on the geometry of the coast from the relatively featureless to the spatially and topographically complex and, against that framework, available substrates from bare rock to finest sediments. The geological literature rarely is presented in these terms, simply because the concerns of geologists and biologists are not the same. Accordingly, the treatment which follows is unconventional. The present section is devoted primarily to consideration of coastal "geometry"; geological substrates are treated separately.

In environmental terms, shorelines are either in direct contact with the open sea or protected within inlets of varying size and configuration. Open seashores may range from simple fronts at scales of tens of kilometres, to strongly featured shores at a variety of scales according to geology and the nature of the environment over time. Whether directly open to the sea or not, topographic gradients and limits immediately above and below mean sea-level are highly variable.

Table 2.2, compiled from Galloway (pers. comm.) provides a useful summary of the geometric structure of the Australian coast at the 0.1 km scale of Galloway & Bahr (1979). Care is needed in interpretation, however, because the data do not refer to the coastline *per se* but to coastal lands within three kilometres of high tide.

Each type of landform listed is represented in every State. Overall, low relief predominates, only 10.4% of coastal lands being characterized as high, rocky terrain. Even so, roughly 18% of the land-sea interface constitutes "cliffs" although it should be emphasized that structures as low as two metres in height are included in that classification.

2. MARINE ENVIRONMENT

In any event, the open coasts, those directly fronting the sea, clearly comprise a variety of land forms within which a matrix of physical elements may be recognized at the scales used. Coastal cliffs, whatever their vertical dimension, range from almost monotonous ramparts to highly sculptured or broken features. The general profile may be interrupted in a variety of ways and at a variety of scales both above, at and below the waterline. Beaches reach their limits as minor features between rocky headlands of low or high relief and, at the other extreme, dominate the landscape as long, featureless fronts to the sea. In the latter case, subtidal gradients are generally undramatic and may be quite extensive. Extensive subtidal gradients and monotony at the shoreline are also true of beach ridge plains and coasts where intertidal and supratidal mud is extensive. Oddly, as Thom (1984) and others have remarked, interest in rocky shores, and more specifically, shore platforms, seems to have diminished over the last 10 to 20 years. An introductory text by Bird (1976) provides a useful account of the morphology of cliffs and their associated platforms with many examples taken from Australian coasts. A systematic or fully detailed treatment of Australian cliffted coasts, or indeed, of Australian rocky shores in general, has not been undertaken, however, except at the scales addressed by authors such as Davies (1977). The range of lithologies and structures, as well as the conditions to which those structures are exposed, is considerable. For sedimented shorelines, substrates rather than spaces are the significant environmental variable and these will be considered in a later section.

At this point, to turn from open coasts to the more protected environments created by semi-closed embayments, estuaries and lagoons is appropriate.

Based on Galloway's data (1981), some 7.6% of Australia's coastal lands may be estimated to be occupied by estuarine and lagoonal waterways with another 14.2% classed as intertidal mud. The total (over 20%) is conservative, since the area included stops at waterways <1 km in width upstream. There are many locations, especially in northern Australia, where estuarine conditions extend a good deal further upstream. Even so, the environmental significance of these features will be obvious and this is reflected in the interest they have generated among geomorphologists and others.

For the purposes of this account, such coastal features are defined as structures at and near the coast which permit the entry of seawater, whether or not it is diluted by freshwater, and which offer some degree of shelter to part of the marine community from the open ocean. The circumstances under which waters of this kind occur vary quite widely, but fit a pattern underlain by geomorphology and its processes as influenced by hydrologic regimes associated with the prevailing sea-levels. For general reference, Bird (1976) and the review papers compiled under the editorship of Lauff (1967) and Schubel (1971) are useful. For Australia, treatments by Rochford (1959), Jennings & Bird (1967), Roy (1984) and several other papers in Thom (1984) are pertinent. A series of 17 monographs prepared by Messel and colleagues (see Messel *et al.*, 1981) provide valuable data on the tidal river systems of northern Australia.

An increase in sea-level, such as followed the last glacial, or a lowering of the land surface will lead to marine transgression. The extent and configuration of the inundation, of course, will depend on the physiography of the region affected. Thus, the form of water-bodies such as Port Phillip Bay in Victoria and Port Jackson in New South Wales are distinctively different. The variety to be found in embayments, estuaries and lagoons around the Australian coast does not depend simply on sea level in relation to existing topography. Their present state is a reflection of the conditions which have prevailed over time, according to location and the nature of the geological foundations upon which they

lie. Jennings & Bird (1967) specify a number of factors as important, including:

1. run-off from the land;
2. wave climate;
3. tidal behaviour;
4. biotic influences;
5. the mineralogy and susceptibility to erosion of coastal sedimentary deposits; and
6. neo-tectonic effects.

The estuarine condition is commonly one of evolution, from very slow to often relatively quite rapid transition from marine to essentially terrestrial settings. As a particular example, Woodroffe *et al.* (1985) found that the estuary of the South Alligator River in the Northern Territory is now much more limited in extent than once was the case, the result of active deposition from the land. Elsewhere, the existence of lagoons, created by barrier formation at river mouths, is an indication of transience, however slowly these changes may be taking place. Over even modest scales in geologic time, the sheltered waters of the coast, as they presently exist, must be considered an ephemeral part of the marine environment. Detailed synthesis of New South Wales estuarine geomorphology is made by Roy (1984), for northern Queensland by Grindrod & Rhodes (1984) and by Thom *et al.* (1975) and Seminiuk (1981a) for northwestern Australia. For recent work in Victoria see Reinson (1977). Studies by Chappell & Grindrod (1984) and by Rhodes (1980) on chenier plains and coastal progradation in the Australian tropics are also relevant, as is a report on Broad Sound, Queensland by Cook & Mayo (1978).

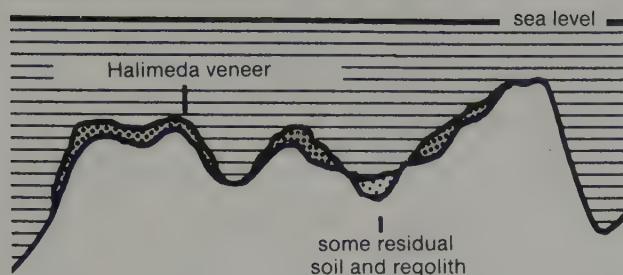
Coral Reefs

Structures created by living corals and associated carbonate depositing species are a distinctive physical feature of the marine environment. Fortunately, considerable attention has been paid to coral reef geology, with excellent reviews of current developments in Baker *et al.* (1983) and a comprehensive account of the subject by Hopley (1982), building on earlier foundations (e.g. see Maxwell, 1968).

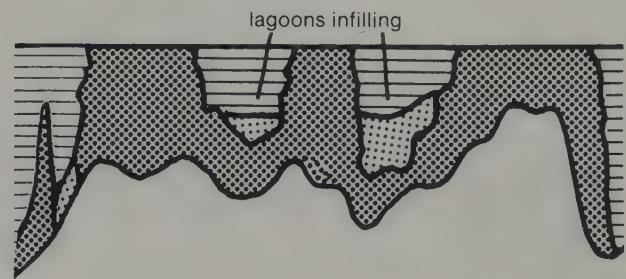
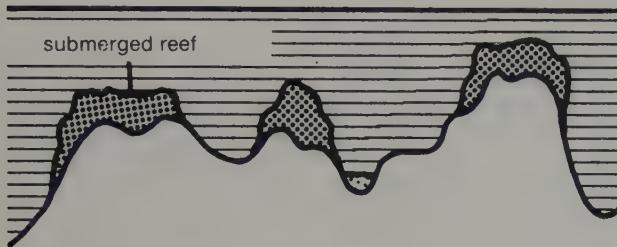
A coral reef is at once a structure, a living community and a self-created environment. At the same time, as physical entities, reefs create what might be termed environmental spaces in adjacent waters and influence the environments of nearby coasts. In this sense, the Great Barrier Reef affects the waters and coast as well as the entire continental shelf of northeastern Australia. While the smaller coral reefs dotted around the northern coastline of the continent and the fringing reefs found along parts of the northwestern coast are less significant regionally, they are important within their spheres of influence.

The Great Barrier Reef extends a total distance of over 2,000 km and is comprised of some 2,500 individual formations. Considered as a coherent structure, it makes possible the existence of a single vast lagoon between its own inner boundaries and the coastline to the west. Large numbers of individually much smaller lagoons are associated with particular reefs as an integral part of the overall structure. With the exception of a small number of high islands, sand spits and vegetated cays, the entire Great Barrier Reef is submerged at high tide. Many of the high islands support well-developed fringing reefs. The latter are also developed to varying degrees on parts of the mainland coastline of Queensland, extending to the Northern Territory and notably on the coast of Western Australia in the vicinity of North West Cape.

Juvenile



Mature



Adolescent

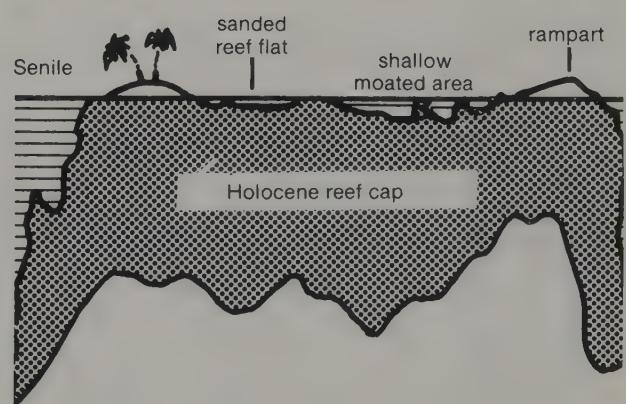


Figure 2.5 The natural progression of reef development from juvenile shown as a cross section through a reef at different times. This pattern would be found on medium-sized reefs, smaller reefs would not include a lagoonal phase while larger reefs may have several lagoonal cells. (After Hopley, 1982)

Holocene shelf reefs within the Great Barrier take a variety of forms, for which the origins of some are not fully understood. Evidence for the influence of pre-Holocene topography, however, is strong. For medium-sized antecedent platforms, a natural progression in reef development from juvenile to senile may be recognized. The stage of development depends upon the topographic height of the original substrate in relation to depth of inundation following marine transgression, each stage having characteristic features as illustrated in Fig. 2.5 taken from Hopley (1982) and summarized by Davies (1983) as follows:

Juvenile: perimeters subtidal, growing vertically; interspersed patches of dominantly branching coral.

Adolescent: perimeters intertidal having recently reached sea-level.

Features include

1. incipient algal flat
2. well-developed coral flat
3. deep, open lagoon
4. no appreciable rubble
5. little sediment leeward
6. incipient prograding subtidal sand sheets

Mature: perimeters intertidal and supratidal. At sea-level for appreciable time.

Features include

1. perimeters exposed at low tide
2. rubble ridges at margins
3. sand/rubble cays unstable
4. windward flats bare
5. coral flats spreading back over sand sheets
6. lagoons moated
7. lagoons open or with patch reefs
8. extensive sand sheet prograding & partial lagoon infill
9. extensive sediment leeward
10. coral profuse on lee flat

Senile: most of reef surface intertidal/supratidal.

Features include

1. windward margins eroding
2. original high rims eroded with remnant blocks windward & leeward
3. lagoon infilled
4. island prograding windward & leeward
5. leeward lagoon margin marked remnant feature.

The gross features displayed in Fig. 2.5 thus conceal a wide variety of structures at lesser scales created by the living corals and their remains. Indeed, the structures to be found in the Great Barrier Reef and the spaces they define present

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Table 2.3 Coastline lengths for materials at the water's edge (km).

STATE	SAND	MUD	AEOLIANITE
Queensland	3 574	1 714	-
New South Wales	1 168	14	-
Victoria	1 112	177	68
South Australia	2 045	281	424
Western Australia	4 766	1 985	472
Northern Territory	2 195	2 308	22
Tasmania	1 061	32	-
Total	15 921	6 511	986

a set of environmental elements which ranges in scale almost continuously from the geographically significant to the microscopic.

PHYSICAL SUBSTRATES IN THE MARINE ENVIRONMENT

So far, this account of the Australian marine environment has been concerned essentially with identifying its larger spaces, as revealed by geographic statistics, the knowledge accumulated by geologists on the continental margins and by geomorphologists on the shelf and at the coast. It is necessary now to deal with finer scales and, in particular, to the physical conditions associated with sediments in the sea accessible to living organisms. In doing so, surfaces must be considered as an element of environment. Indeed, attention to surfaces may provide at least a conceptual link between the scale used by Galloway & Bahr (1979) in measuring coastlines and the scales needed for studying smaller features or structures. In terms of living environments, the fact that a gap in physical scale must be left between Galloway & Bahr's (1979) 0.1 km and the μm scale of sedimentary materials is inescapable. Little or no scientific attention appears to have been paid to structures and spaces through that transition. In any event, because the notion of surface is to be introduced, this Section is entitled "substrates".

Physical substrates are significant in the sea because they present surfaces on which living things may grow. Where those substrates are particulate, they not only offer attachment but also a structurally and spatially peculiar set of habitat conditions for the species adapted to living in them.

Rocky Coasts

The simplest and most durable of surfaces exist in exposures of rocks which offer reliable anchorage or base for a variety of marine algae and a considerable range of animals. Other rocks, whose structure and lithology predispose them to more rapid physical and/or chemical degradation offer surfaces which are rather less reliable but these, too, are widely colonized. Indeed, their texture and often more complicated surfaces may even provide better haven than more permanent but plainer substrates.

Australian shores offer a variety of rocky surfaces. In the south and east, sandstones, shales and limestones are common. Granitic and other igneous formations are widespread along the coast of Queensland and some of its offshore islands. Laterites commonly outcrop along more northern

shores. Precambrian rocks dominate the Kimberley coast of Western Australia. Comparative accounts of such outcrops, as physical substrates, are not available for Australia.

Living Substrates

Living organisms, whether or not associated with rocky substrates, may provide a solid physical base for other species. Among many examples are the substantial flora and fauna associated with the trunks of mangrove trees and the epiflora and fauna of seagrasses and marine macroalgae. A synthesis of information on this topic in an Australian context has never been undertaken.

Sediments

There has been wide interest in the nature of superficial sedimentary deposits in the Australian marine domain. Most treatments, however, approach sediments as geological entities rather than in terms of their physical properties as surfaces and creators of fine space for occupation by living organisms.

Among many treatments of Australian sedimentary sequences, a concise account by Doutch & Wilford (1979) provides useful orientation. Here, it need be noted only that sedimentary deposits of varying age, origin, structure and lithology dominate most of the coast and continental margin. Unconsolidated or weakly consolidated facies of recent origin overlie a great deal of the antecedent sea bed and shoreline foundations. Those are the immediate concern of this account.

Shoreline and Nearshore Sediments. Sandy shores are distributed widely (Table 2.3) and more than twice as extensive as those classed as muddy, which are most common in the north. Intertidally, the extent of muddy surfaces is considerable, especially in the tidal plains of the tropics.

Most physical studies of coastal sands tend to be related to the susceptibility of sands to transport by currents, waves and wind and to their collective fate through time. Their textural properties are largely treated in such a context. Whether composed primarily of quartz or carbonates, they vary widely in texture and those properties are well known to influence their suitability as habitats for any one of many particular sand-dwelling communities. In view of the widely scattered, diverse and largely superficial literature, seeking an overview of sands as habitats in Australia would be impractical. For a current world view, see McLachlan & Erasmus (1983).

Broad background on the physical properties of muddy sediments is provided in a review volume on Holocene sedimentation edited by Klein (1976) and another on coastal sedimentary environments edited by Davis (1978). For general accounts of soils associated with salt marshes and mangroves, the two major communities occupying muddy substrates, Ranwell (1972), Macnae (1968) or Walsh (1974) should be consulted. No review of Australian conditions is available.

Studies reported by Reinson (1977) in Mallacoota Inlet, a temperate estuary, indicate that the sediments at that location vary widely in textural character from mud to gravelly sand. Within that range, the content of silt increases from <5 to >40% and of clay from <20 to >50% by weight. Mud is widely distributed within the estuary, but is dominated by silt in the upper reaches and by clay in the lower.

Textural variety of this kind is a common feature of many estuarine sediments. In Broad Sound, Queensland, for example, Cook & Mayo (1980) recognize four units, including (1)

unsorted mixtures of gravel-sand-mud, (2) partly sorted sand and mud, (3) well-sorted sands of high-energy conditions and (4) muds sorted under low-energy conditions. Muds, however, are certainly more predominant and extensive within coastal environments of the Australian tropics. Of four types of clayey salt pan and tidal flat soils recognized by Northcote *et al.* (1960–68), only one has extensions into southern latitudes, notably in parts of South Australia.

Within the tropical zone, coastal muds in the northwest have been described by Thom *et al.* (1975) and by Semeniuk (1981b); in the Gulf of Carpentaria by Rhodes (1982) and in northern Queensland by Chappell & Grindrod (1984), Grindrod & Rhodes (1984), Boto & Wellington (1984) and others.

On a chenier plain coast in the Gulf of Carpentaria, Rhodes (1982) distinguishes muds as high-tidal, intertidal, low-tidal and subtidal with the former containing, on average, 50% clay and the latter, variable percentages of sand and silt and up to 50% calcium carbonate. Generally similar suites of sediments have been described elsewhere, although fine differences in sediment character, presumably due to relative differences in silt, clay and organic content are recognizable from location to location. At extremes, some muddy sediments are reasonably well consolidated while others, especially intertidally, are virtually oozes.

Sediments of the Shelf, Continental Margin and Abyssal Sea Bed. Detailed studies by Connolly & Von Der Borch (1967) and Wass *et al.* (1970) reveal that on its southern margins, the continental shelf is covered with "coarse calcareous and mainly relic Pleistocene sands" essentially composed of the remains of bryozoans, molluscs and other calcareous species. Living Bryozoa, which contribute new material to the sediments are associated selectively with them according to their granularity. The materials have been re-worked to varying degrees and modal grain sizes range widely from 0.03 to 10.0 mm. Foraminiferal tests and sponge spicules become abundant with bryozoan remains on the upper slope while foraminiferal and coccolith oozes predominate on the slope proper. The surface sediments of the abyssal plain are difficult to describe in summary although the term silty clay would seem appropriate. Notably, the upper 50 to 150 mm were found to be burrow mottled.

A comprehensive survey within Bass Strait and on the continental shelf around Tasmania reported by Jones & Davies (1983) indicates four principal classes of surface sediment in that region. Bryozoan sands and gravels occupy the outer shelf of the west and southern coast with extensions along the east and within parts of eastern and western Bass Strait. Closer by the coast, as well as around King Island and extending in the east around Flinders and Cape Barren Islands on to the southeastern coast of Victoria, quartz sands with variable amounts of modern shell debris predominate. Several pockets of fine-grained shelly sands occur in the south as well as off Port Phillip in Victoria and at one location in eastern Bass Strait. Muddy quartzose and calcareous sediments, largely in areas of modern deposition, occur sporadically along the eastern coast and also in central Bass Strait. Grain size distributions determined for each of 365 samples from the survey show the following ranges in composition:

% Gravel	0.00–88.19
% Sand	2.34–99.58
% Silt	0.00–45.73
% Clay	0.00–11.44.

The surface shelf sediments further north along the southeastern coast of the mainland, are largely relict (Davies, 1979). They are terrigenous in origin closer to the coast with carbonates increasing with depth below 60 metres. Kaolinitic

and chloritic muds exist in distinct zones at mid-shelf. Most of the shelf sediments, however, are sands. Roy & Thom (1981) maintain that aeolian sand deposits in southern Queensland have their origin in the coastal sediments of New South Wales which have been subject to northerly transport over a number of glacial-interglacial cycles. Marshall (1980), in fact, has found that sands predominate on the continental shelf of northern New South Wales and southern Queensland and considers the sediments as a whole to be relict. He notes that gravels, as well, have a wide distribution, sometimes exceeding 60% of total sediment. Carbonate content increases generally from the inner to outer shelf. Four types of quartz sediment have been recognized, based on criteria of grain size, degree of roundness and sorting.

A great deal of information is available on the superficial sediments of the Queensland continental shelf within the Province of the Great Barrier Reef and Lagoon. This is reflected in a comprehensive account by Maxwell (1968). Additional detail is incorporated in a recent text by Hopley (1982) and in an account by Orme & Flood (1980).

Essentially, sediments generally characterized by mud dominate the inner shelf and receive significant contributions from terrigenous sources. Exceptions, however, are not uncommon with areas of fine to coarse quartz sand, gravels and pebbly materials all represented. Carbonate concentrations also occur inshore, but these materials are general on the outer shelf and predominant there. This is true also of reef flats, of course, and lagoons in which more finely divided deposits are typical. Carbonate shingle banks are found on reef crests and rims. Differences in faunal composition have a marked influence on the nature of reef sediments. To appreciate the nature of such variety and its sharp transitions, reference should be made to Maxwell's (1968) charts.

The surface sediments of the Gulf of Carpentaria are green muds and silts rich in marine faunal remains (Phipps, 1966). On the adjacent Arafura Shelf, Fairbridge (1966) considers the surface sediments as glauconitic sand and calcareous mud. Closer by the coast, however, hard bottoms indicate general paucity in sediment supply, especially since tidal currents are only moderate. At the same time, terrigenous muds appear to occur in the associated Aru Trough, although the slopes of the Trough are mantled in globigerinal ooze.

Further to the west, Van Andel & Tjia (1966) indicate that the sediments of the Sahul Shelf in the Timor Sea are largely relict, predominantly calcareous and coarse-grained. Bryozoan remains are abundant, although *Halimeda* sediments characterize shelf-edge banks. Finer carbonates occur in the Bonaparte Basin and in estuaries on the adjacent coast. Sediments of the Timor Trough are mostly silty clays interbedded with foraminiferal sands.

On the continental shelf of Western Australia further to the south, as on the Arafura Shelf, little sedimentation appears to be taking place at present (Jones, 1971). Calcarenite occupies the main shelf with finer grained foraminiferal sediments at the shelf-edge. The adjacent sea bed is predominantly red clay (Fairbridge, 1966). For a global review of conditions on the abyssal sea floor, see Menzies (1965).

As a final comment, and returning to an introductory observation that although marine sediments are well-acknowledged to have strong faunal and, in shallow water, floral associations, detailed studies of their physical properties as an environment for marine organisms are exceptional. Sediment condition is certainly taken into account by benthic ecologists, but generally without rigorous support of the kind offered by soil physicists to those concerned with these materials as living substrate for plants and a distinctive infauna on land. Thus, this account of marine sediments cannot be

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extended beyond rather broad characterization of textural and related properties. Sediment geochemistry will be considered in a later Section.

THE SEAS AROUND AUSTRALIA AND AT ITS COASTS

The basic attributes of the sea as an environment are its motions at various scales through time and its variable intrinsic physical properties. Motion within the sea and at its surface, in turn, delivers the capacity to shape its boundaries, notably at the coast, and modify their physical condition. This Section is devoted to a consideration of the seas around Australia in those terms. To the extent possible, the subject will be treated within regional settings recognizing, however, that some phenomena, especially those of small scale, particular interest or limited study, may demand individual consideration.

General Circulation and Principal Water Masses

The waters which touch or pass along the continental boundaries do so as part of a global circulation and most directly through motions within the Pacific, Indian and Southern Oceans and subsidiary seas including the Tasman and the Coral to the east and the Timor and Arafura to the north and northwest.

By atmospheric forcing under the influence of the earth's rotation and with modifications induced by the disposition of the continental land masses, general circulation towards the surface of the major ocean basins is in the form of large gyres. In the South Pacific and Indian Oceans, movement within the gyres is counterclockwise and consonant with flows associated with equatorial currents in each ocean. Close to or around the equator are counter currents flowing to the east. A comparable but far more substantial easterly flow in the Southern Ocean is sustained by the prevailing westerlies. Complete circulation within each of the major gyres, according to Turekian (1976), is achieved within rather less than 10 years, while exchanges between the Indian and Pacific Oceans occur via the circumpolar Southern Ocean and in a more complex manner to the north of Australia and through the islands of Indonesia. In the deep ocean, the circulation is of rather a different kind and driven by thermohaline gradients initiated in the polar regions. Its details in waters around Australia are not well understood. Stommel (1957), however, infers a western boundary current skirting New Zealand to the east and flowing northward with return predominantly arcing to the east. A similar eastwards movement towards the western coast of Australia is believed to originate in a northward flowing boundary current to the east of Africa and Madagascar. Turekian (1976) indicates that the residence time of waters in the deep Pacific is probably 1,500–2,000 years. For further information at large scales, the reader would find it useful to consult Tchernia (1980).

The Regional Scale

This consideration of the Australian seas conveniently begins with the waters of the Coral and Tasman Seas and adjacent continental shelves, followed by the eastern parts of the Indian Ocean including the Australian shelf. Separate treatment of northern waters enables some consideration of interchanges between west and east. The Section concludes with attention to the ocean south of Australia. Some topics will be excluded from the regional setting and treated individually in a separate Section.

The Coral and Tasman Seas

Seas beyond the Shelf. The principal motions at and near the surface in the Coral and Tasman Seas are part of the general circulation of the South Pacific. Flows along the eastern coast of Australia, however, appear to be rather more complicated than in the much more clearly defined current systems of ocean basins in the Northern Hemisphere. The details of earlier studies may be found in a review by Rotschi & Lemasson (1967) while a more recent overview by Hamon & Golding (1980) provides useful perspective.

Description of the temperature, salinity relationships of the surface and subsurface water masses of the Coral and Tasman Seas would not be feasible in the space available. Salient features, however, have been summarized in Table 2.4, (see Rotschi & Lemasson, 1967). A comprehensive review of the physical oceanography of the western Coral Sea has been prepared by Pickard *et al.* (1977).

According to Pickard *et al.* (1977), many features of the circulation within the Coral Sea remain uncertain. Essentially, however, major input occurs north of 15°S and is derived from the South Equatorial Current supplemented from the east by a general inflow south of 20°S. Outflow follows to the north and then west into the Solomon Sea and southwards into the East Australia Current. The nature of the circulation within the northwestern Coral Sea is not well understood. Figure 2.6 indicates mean circulation at several depths throughout the Coral Sea. Note some inflow from Torres Strait indicated during the summer period.

Considerable attention has been paid to the southward flow from the Coral Sea, designated the East Australia Current. Early work by Wyrtki (1960) has been sustained by a number of investigators up to the present time. Boland & Church (1981) describe the flow as an "episodic, intense western boundary current flowing southward along the continental slope from about 27°S." At various locations, but notably around 33°S, the current separates from the coast and turns out to sea. The sharp fronts which result at the interface of the southward flowing warm waters and cooler southern waters have been described by Cresswell *et al.* (1983). Moving eastward, the conjunction of Tasman and southern Coral Sea waters is evidenced in the Tasman Front, which extends from Australia to the north of New Zealand. Studies by Andrews *et al.* (1980) have revealed considerable excursions of the Tasman Front with the formation of equatorward cyclonic meanders and poleward anticyclonic meanders with a latitudinal spread of 400 to 700 km.

Studies by Godfrey *et al.* (1980) indicate that the behaviour of the East Australia Current differs to the north and south of around 33°S. To the north, flow patterns appear to be "open" or related to large, elongate eddies. South of 33°S, the warm-core anticyclonic eddies shed from the current are comparatively small and circular. Topographic control is suspected. From earlier discussion, the observation is recalled that separation of the East Australia Current from the coast is associated with clear differences in the sediment regime of the continental shelf north and south of 33°S, an interesting example of circulation patterns influencing sediment transport and deposition.

The eddies which progress generally southward after formation around 35°S have been studied by a number of oceanographers to whose work reference may be found in a recent account of one such structure by Cresswell (1983). Characteristically, the eddies have diameters around 200 to 300 km, exhibit rotational velocities of up to approximately 1.3 m sec⁻¹ and, once formed, may persist for at least a year. There is evidence that they may be detectable as entities to depths as great as 1,500 metres. Mixing at the centres may extend to 300 m in winter. Boland & Church (1981) undertook detailed

Table 2.4 Principal primary and derived water masses in the Coral and Tasmanian Sea region. (After Rotschi & Lemasson, 1967)

	CORAL SEA	SUBANTARCTIC	TASMAN SEA (Central)	TASMAN SEA (Southwest)	N.Z. (Centre)	TASMANIAN Coasts
S‰	35.41-35.59	34.60-34.87	35.50-35.68	35.23-35.41	34.51-34.87	35.05-35.23
T°C	20-26	10-14	15-20	12-15	15-20	10-14
Origin	N.W. Coral Sea	Australia Ocean	Tropical Convergence	East of Bass Strait	East of Cook Strait	Coast of Tasmania
Nature	Primary, external	Primary, external	Primary, internal	Derived	Derived	Modified
Formation	Mixture of South Equatorial and Central Pacific Water	Rewarmed Antarctic Water	Rewarmed Coral Sea Water	Mixture of Central Tasman and Sub- antarctic Waters	Rewarmed Subantarctic Water	Diluted by run-off
Season of maximal extension	October May	May September	June December	June December	April December	April December
Region of extension	Western Tasman Sea	Surface south of 45°S	Southern Tasman Sea	South of 38°S., southwest Tasman Sea	West of North Island, Tasman Sea	Coast of Tasmania New Zealand

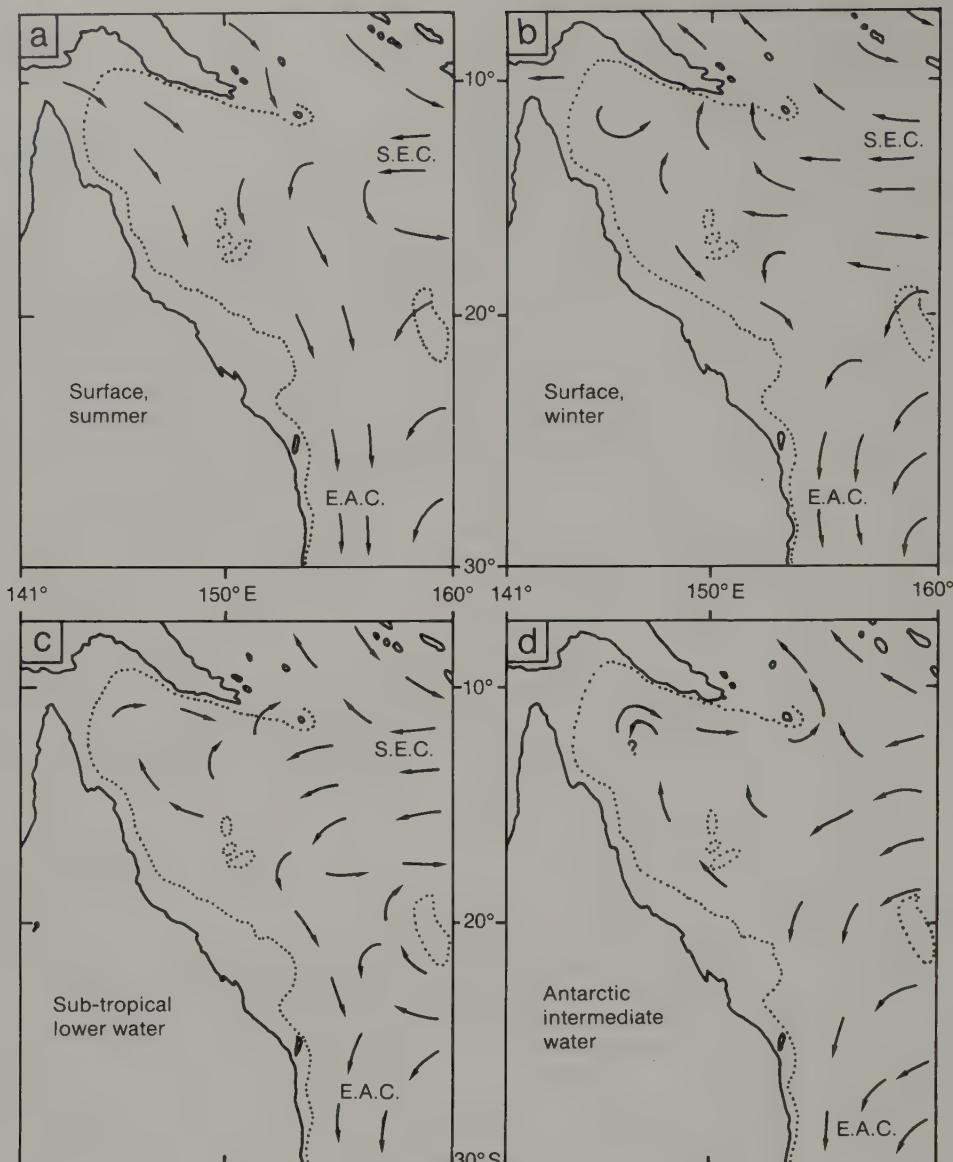


Figure 2.6 The mean circulation patterns of the western Coral Sea at the surface in summer (a) and in winter (b). The circulation of Subtropical Lower Water (salinity > 35‰), which has a core depth of 50–250 m and a layer thickness 200 m, is shown in (c). The circulation of Antarctic Intermediate Water (salinity < 34.5‰), which has a core depth of 650–1150 m and a layer thickness 400 m, is shown in (d). (After Pickard *et al.*, 1977). EAC = East Australia Current, SEC = South Equatorial Current.

studies of the eddy fields and their evolution in the course of a single year, but indicate that they could not be sure that their observations were representative in the longer term. The complexity of eddy behaviour has been discussed in some detail by Nilsson & Cresswell (1981). The principal features of the East Australia Current system are illustrated in Fig. 2.7 provided by Dr J.C. Andrews.

The Sea of the Eastern Continental Shelf. With a change to finer scales, there is even more difficulty describing the physical processes and conditions both within the sea and relevant to it as an environment for life. What follows treats briefly, first the waters of the Great Barrier Reef and then the continental shelf further to the south.

Andrews (1983a;b) demonstrated regular intrusions of subtropical lower water across the shelf break of the Great Barrier Reef with temperatures 1 to 4.5°C cooler than lagoon water and associated with slope waves of a period near 90 days. Wolanski & Pickard (1983) obtained evidence of inter-

nal tides with vertical displacement of up to 100 m and basically solar semi-diurnal in period. Tidal upwelling of another kind, which occurs through narrow reef passages, is reported by Thompson & Golding (1981). The ecological consequences of upwelling events in the region are considerable and have been investigated by Andrews & Gentien (1982).

On the shelf occupied by the Great Barrier Reef and its principal lagoon, Wolanski & Bennett (1983) and Wolanski & Pickard (1983) observed several components of the current. Those driven by the tides are relatively weak ($<0.2 \text{ m sec}^{-1}$). In the central section of the province, on the other hand, wind-generated low frequency longshore currents, moving primarily northward, exhibit fluctuations $<1 \text{ m sec}^{-1}$ and are responsible for considerable excursions of water up and down the coast. These motions operate in face of a $\approx 0.3 \text{ m sec}^{-1}$ shelfwide poleward flow linked with the East Australia Current which prevails on the upper continental slope everywhere south of 14°S. The modifying influences of reef topog-

raphy on shelf circulation in the northern Great Barrier Reef have been explored by Wolanski & Ruddick (1981) who, in course of that study, also detected the influence of low-salinity plumes from the Gulf of Papua as far south as 12°30'S at the coast. Further details of the wind-driven circulation in this topographically complex region are given by Wolanski & Thomson (1984) and Wolanski *et al.* (1984b).

Turning to the continental shelf further south than the Great Barrier Reef, very long period (*circa* 120 days) motions have been well recognized since the work off the coast of New South Wales by Hamon (1962) who, with others, attribute their observations to meanders in the East Australia Current. Shelf waves of shorter period were ascribed to longshore wind stress (Hamon, 1976). In addition to long period motions (*circa* two to four days) along the same coast, the East Australia Current also is known to be associated with frontal phenomena which extend over the shelf and into the Tasman Sea. These features incorporate wakes at headlands and islets and involve northward flowing cool littoral countercurrents. Cresswell *et al.* (1983) observed breaking waves at the front and an abrupt temperature change at the interface of 2.5°C, noting that such locations are known to attract schooling Bluefin Tuna to feed.

Physical processes of other kinds have been examined for the southern continental shelf, including internal waves (Cresswell & Boland, 1981) and upwelling (Rochford, 1975).

The Southeast Indian Ocean

The physical properties of the water masses in the Indian Ocean as a whole are described in some detail by Tchernia (1980), while Rochford (1961; 1962; 1964) comprehensively treats the upper and intermediate waters of the southeastern sector as well as the surface layers in spring and summer.

Briefly, Tchernia (1980) recognizes five principal water masses in the southern part of the Indian Ocean which are maintained to as far north as 10 to 15°S. These include:

- a. bottom water: 0.5°C; S = 34.70 to 34.72‰
- b. deep water: 2.0°C; S = 34.7‰
- c. Antarctic intermediate water: 5.0°C; S = 34.50‰
- d. central water; 10.0 to 15.0°C; S = 34.70 to 35.60‰
- e. surface water; variable according to region.

In the upper 500 m, Rochford (1964) found four water masses identifiable with waters in the northern Indian Ocean *viz*: Red Sea, Persian Gulf, Arabian Sea and a so-called water mass E as well as a "salinity maximum F" entering the region west of Sumatra and distributed north of 15°S. A major entity named the "south east Indian high salinity water mass" occurs south of about 20°S.

Surface circulation within the region is complex and still incompletely understood (Hamon & Golding, 1980). As Phillips (1982) points out, the eastern limit of the Indian Ocean adjacent to Australia is unusual in that its boundary current lacks clear structure and has a poleward rather than an equatorward flow. Evidence for such a southward flow of tropical water stems from early observations by Saville-Kent (1897) of tropical marine fauna around the Houtman Abrolhos Islands. The Leeuwin Current, as it is now known, has been identified and studied from satellite infrared imagery (Legeckis & Cresswell, 1981). Sea surface temperatures in Figure 2.8, from that study, reflect the current throughout its range.

Most pronounced over the autumn and winter (from May to September), the current may be traced from a source off northwestern Australia, continuing first along the shelf from

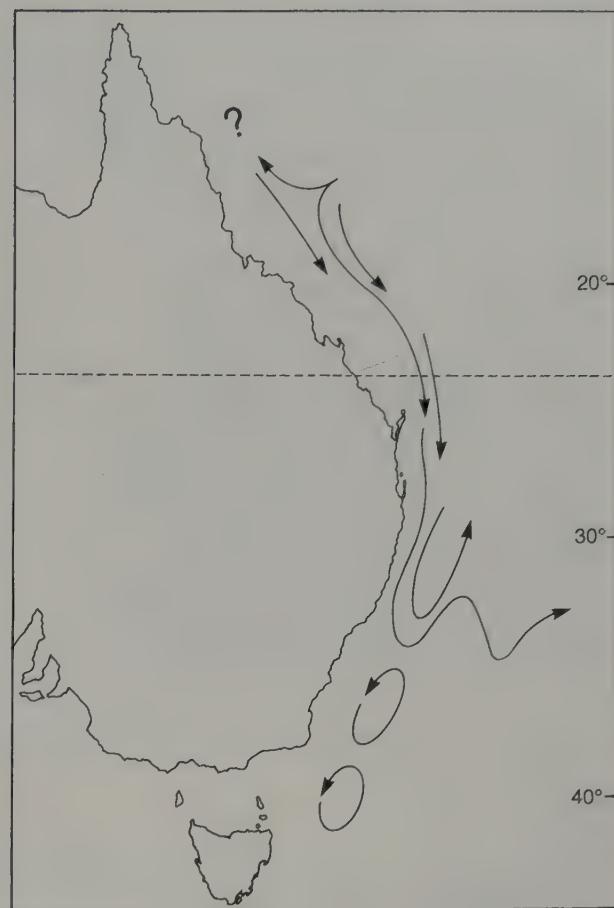


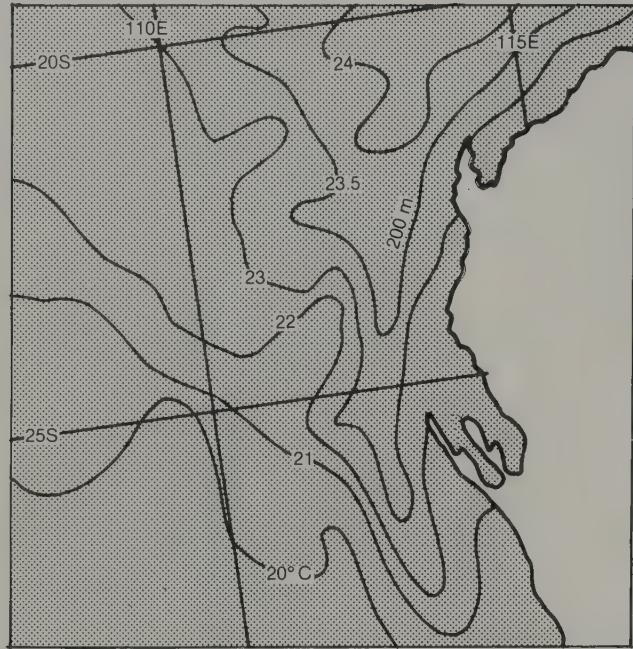
Figure 2.7 A diagrammatic representation of the major features of the East Australia Current system (see text for explanation). (Compiled by J.C. Andrews after Andrews *et al.*, 1980; Boland & Church, 1981; Nilsson & Cresswell, 1981)

22 to 27°S and then over the continental slope to beyond 29°S. At Cape Leeuwin, the flow diverts eastward, largely on the shelf, where it may be seen to extend completely across the Great Australian Bight (Maxwell & Cresswell, 1981; Legeckis & Cresswell, 1981). An analysis by Thompson & Veronis (1983) indicates that the system is generated by wind stress over the northwestern slope of Australia during the autumn/winter period. In summer, the tropical low-salinity water continues its passage from the north, but also carries high-salinity water introduced from the west (Andrews, 1977).

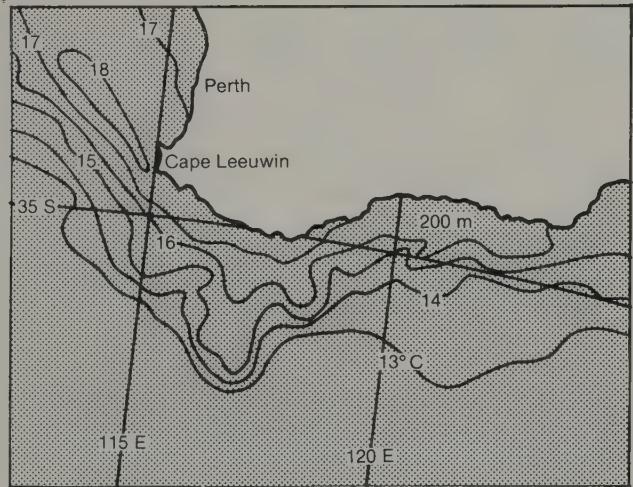
The general flow of the Leeuwin Current is associated with, and complicated by, the formation of eddies and fronts, the structures of which appear to vary seasonally. A study of conditions off the coast from Perth in summer by Andrews (1983c) indicates the existence of both warm- and cold-core rings. Features of this kind are predominantly, but not exclusively, cyclonic (Cresswell & Golding, 1980). In its eastward extension across the Great Australian Bight, Legeckis & Cresswell (1981) found large scale seaward offshoots of the current evident in satellite imagery. The more detailed behaviour of the Leeuwin Current remains a source of considerable interest both to biological and physical oceanographers.

The Continental Shelf: Western Australia. Physical processes, including upwelling and wind-driven circulation occurring at a range of scales, are of interest. Evidence of upwelling on the North West Shelf has been presented by Rochford (1962), largely on the basis of increased inorganic phosphate

a



b



c

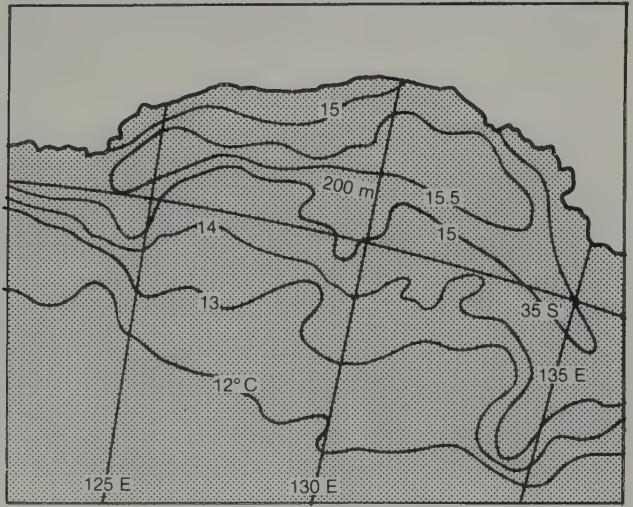


Figure 2.8 The sea-surface temperature contours off the coast of W.A.; a. northwest (for 30 April 1980); b. southwest (for 23 October 1979); c. Great Australian Bight (for 14 July 1979). (After Legeckis & Cresswell, 1981)

levels in the region. Similar evidence also was presented for the eastern Arafura Sea. At the same time, Wyrtki (1962) considers the main upwelling area to lie along the coast of Java and Sumbawa. He estimated $2.4 \times 10^6 \text{ m}^3 \text{ sec}^{-1}$ to be delivered from upwelling to the South Equatorial Current during the southeast monsoons.

On the North West Shelf, nonetheless, the phenomenon has attracted ongoing interest. For example, satellite observations have now been used successfully by Baines (1981) in detecting tidally generated internal waves from North West Cape to the latitude of Darwin. Wavelengths were in the range 300 to 1,000 m with current speeds in an onshore direction of 0.5–1.0 m sec⁻¹.

Concerning wind-driven circulation, other than that associated with cyclones which will be considered elsewhere, studies in the large embayment of Cockburn Sound by Steedman & Craig (1983) are pertinent. Under those conditions, tidal currents were found to be weak. Observed mean velocities of less than 0.05 m sec⁻¹ were essentially wind-driven although storms caused increases up to 0.25 m sec⁻¹. Local density gradients due to evaporation and heating were responsible for currents up to 0.1 m sec⁻¹ under calm conditions. Daily exchange with surrounding waters under the driving force of winds was small in comparison with the volume of the sound, making it effectively a closed system.

Northern Waters

Pickard *et al.* (1977) account of the western Coral Sea notes the significance of Torres Strait in restricting exchange between Pacific and Indian Ocean waters across northern Australia. An analysis by Godfrey & Golding (1981) indicates a net regional flow-through of order of magnitude $10 \times 10^6 \text{ m}^3 \text{ sec}^{-1}$. The rate is rather larger than earlier estimates and, incidentally, may help account for an anomalous weakness in the East Australia Current. The authors predict, further, that elimination of the flow would significantly influence circulation in the Indian Ocean south of the equator and also could lower surface water temperatures off Western Australia by around 3°C.

The extent to which exchange through Torres Strait is affected by local and perhaps relatively ephemeral bottom topography is therefore of interest. Wolanski & Ruddick (1981) show that continental shelf motions on the Great Barrier Reef are influenced, as one might expect, by reef densities. The effect of the many islands and reefs between Cape York and the western Gulf of Papua, however, does not appear to have been studied. Even precise knowledge of the local currents is sparse.

Apart from an account by Wyrtki (1961), the primary source of information concerning the water masses of the Timor and Arafura Seas is Rochford (1962). Upwelled waters of uncertain origin appear to dominate this region. Some of the water masses, however, are southeastern extensions of the Indian Ocean and, at least at the surface, part of the Tropical Zone suite with a variety of salinity characteristics. The reader should refer to Rochford (1962) for detail.

Gulf of Carpentaria. The continental shelf waters of northern Australia are not well studied, notably within such complex geographic features as the Joseph Bonaparte and Van Diemen Gulfs, although some attention has been paid to the much larger Gulf of Carpentaria. According to Rochford (1966), three principal water masses are associated with the Gulf. One, with salinity 33‰, originates in the coastal region of West Irian, and after monsoonal dilution, drifts into the eastern Arafura Sea and northern Gulf. A second mass of salinity, >35.5‰, is of northwestern Coral Sea origin and reaches the eastern side of the Gulf during winter (see also

Wolanski *et al.*, 1984b), later mixing westward with the waters of low salinity. The third mass evidently derives from subsurface waters in the Banda Sea and is believed to upwell only in restricted areas.

Generally, the waters of the Gulf of Carpentaria are well mixed vertically and are involved in a tidally-induced clockwise circulation which Church & Forbes (1983) and Forbes & Church (1983) report occurs at velocities between 3.7 and 11.8 cm sec⁻¹. Density induced currents at mid-depth range from 1 to 10 cm sec⁻¹. Trade winds are capable of reversing the circulation according to their persistence and strength.

Waters to the South of Australia, including Bass Strait

These seas are most rationally treated within the larger context of the circumpolar Southern Ocean the northern limits of which are generally accepted to lie at the Subtropical Convergence immediately south of the Australian continent. References to the key early authorities for the Southern Ocean, are provided by Kort (1968) and a recent review has been prepared by Tchernia (1980). Westward drift waters reach Australia along the southern half of Tasmania and, during winter, also reach the coast of western Victoria. Further comment is largely restricted to the waters north of the Subtropical Convergence which lies roughly around 40°S and across which temperatures increase from around 10 to 14°C in winter and from 14 to 18°C in summer with a rise in salinity from approximately 34.5 to 35‰. Details of Southern Ocean frontal structures in the Australian region are reported by Edwards & Emery (1982).

In his description of the southeastern Indian Ocean, notably its surface waters, Rochford (1962) considers the sector south of Australia and north of the Subtropical Convergence to be an extension of the Indian Ocean subtropical water mass. Its distinguishing features, however, were high salinities (between 36.30 and 36.50‰) and slightly higher temperature. These and other features indicate extended residence times and a degree of physical isolation. Nevertheless, we now know that the low salinity waters of the Leeuwin Current may be observed to extend into the Great Australian Bight.

At a lesser scale, the circulation within the South Australian gulf system is relevant. A modelling approach used by Tronson (1974) suggests that the circulation is wind-driven, indicating, in Gulf St Vincent, northward transport along the western shore with a circulation cell at the head of the Gulf and separation in circulation along its eastern shore. Under southerly winds, four circulation cells could be associated with Spencer Gulf. Westerlies change that pattern and complete exchange in and out of the Gulf under prevailing conditions is likely very slow.

Bass Strait leads to the Southern Ocean north of the Subtropical Convergence to the west and to the Tasman Sea immediately to the east. The hydrology of the waters around Bass Strait is reported by Newell (1961), indicating surface salinities <35.05‰ to the south and southwest, increasing to >35.59‰ close to the coast of western Victoria and within the southern limits of the East Australia Current system. Within Bass Strait, surface salinities mostly range from 35.23 to 35.58‰ with the higher salinities to the north. They are identified as a complex of the East Australia Current, sub-Antarctic and high salinity waters at the Victorian coast.

Direct observations along the western coast of Tasmania and the western boundary of Bass Strait by Baines *et al.* (1983) have confirmed the current predicted by Thompson & Veronis (1983). It is a narrow, baroclinic and evidently permanent flow running poleward over the slope, but westward over the shelf and is not an extension of the Leeuwin Cur-

rent. In contrast, to the east and at least in winter, Godfrey *et al.* (1980b) discovered the waters of Bass Strait to cascade into the Tasman Sea. The phenomenon is marked by a distinct temperature front at the surface, the flow being detectable at depths up to 400 m in the Tasman. Tomczak (1981) reports that such intrusions may be traced 600 nautical miles along the shelf edge and 200 nautical miles offshore. At the same time, calculations indicate that the amount of water involved is small, although it is estimated that less than six months would suffice to effect complete exchange of the Bass Strait water mass by this means, with replacement occurring from the west.

Several authors have considered the circulation within Bass Strait itself. The most recent and comprehensive treatment of the topic has been offered by Fandry (1983) in the form of a three-dimensional model most applicable under winter conditions, when the area is well mixed vertically. Under those conditions, the predicted wind-driven surface circulation produced a flow at 45° to the left of the wind and was strongly dependent on depth. Tidally induced currents on the western and eastern sides of the Strait, as modelled in absence of wind, were discovered to have opposed flows, leading to very weak tidal motion in the central region. Between King Island and the mainland, tidal currents reach velocities to 2.5 m sec⁻¹. Jones & Padman (1983) have detected internal tides near the eastern boundary of the Strait with amplitudes of ≈40 m, well correlated with surface tides but lagging them by 0–6 hours.

Conclusion to the Section

Notwithstanding the limitations of any simple diagram or tabulation to effectively summarize the physical characteristics of the Australian Sea in time and space, even at major scales, some general frame of reference seems essential. For that purpose, Figs 2.9 and 2.10, showing surface and 100 m salinities around Australia, are presented (from Rochford, 1980) as well as Figs 2.11 and 2.12 showing sea surface temperatures in January and July (from Anon, 1981). Many other parameters and scales are relevant, but these must be sought from the available literature.

PARTICULAR CONDITIONS AND PHYSICAL PROCESSES AFFECTING THE AUSTRALIAN SEA AND ITS WATERS

Run-off from the Land

A total of 225 recognized watersheds in nine drainage basins discharges into the Australian coastal sea (Anon., 1978). The nature of that discharge through time and the manner of its delivery through coastal inlets and waterways of great variety combine to create an environment of enormous diversity. That diversity is further compounded by the action of tides and winds.

Table 2.5, abbreviated from Warner (1977), provides data on the areas of those drainage divisions that reach the coast and of their gross deliveries of fresh water. Several points need to be made. Freshwater discharge into the Gulf of Papua, principally from the Fly, Kikori and Purari Rivers alone amounts to $>40.0 \times 10^{10} \text{ m}^3 \text{ yr}^{-1}$ (Wolanski *et al.*, 1984b). This estimate considerably exceeds a total for Australia of around $30 \times 10^{10} \text{ m}^3 \text{ yr}^{-1}$. Not only does this indicate a substantial influence on Australian northern waters from a neighbouring land mass, it also reflects the general well-known aridity of the Australian continent. Further, the gross figures do not

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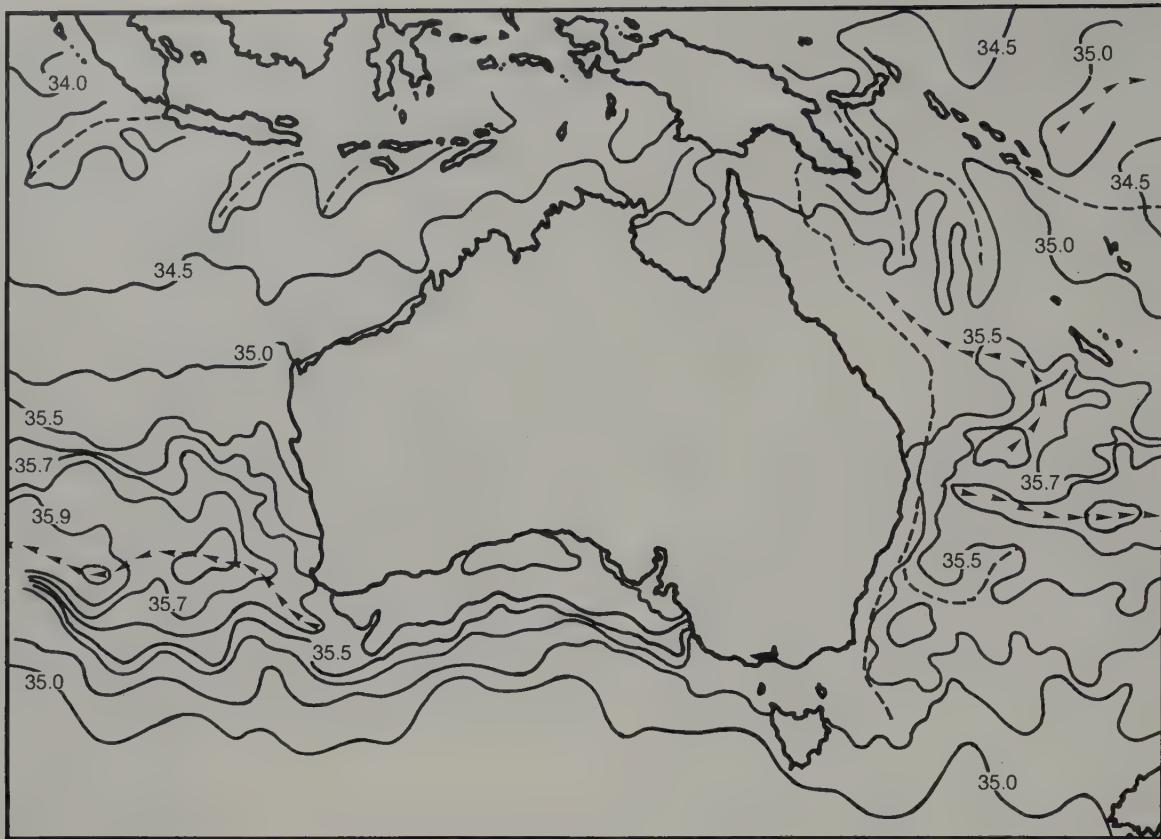


Figure 2.9 The salinity (S‰) at the surface of the oceans around Australia. (After Rochford, 1980)

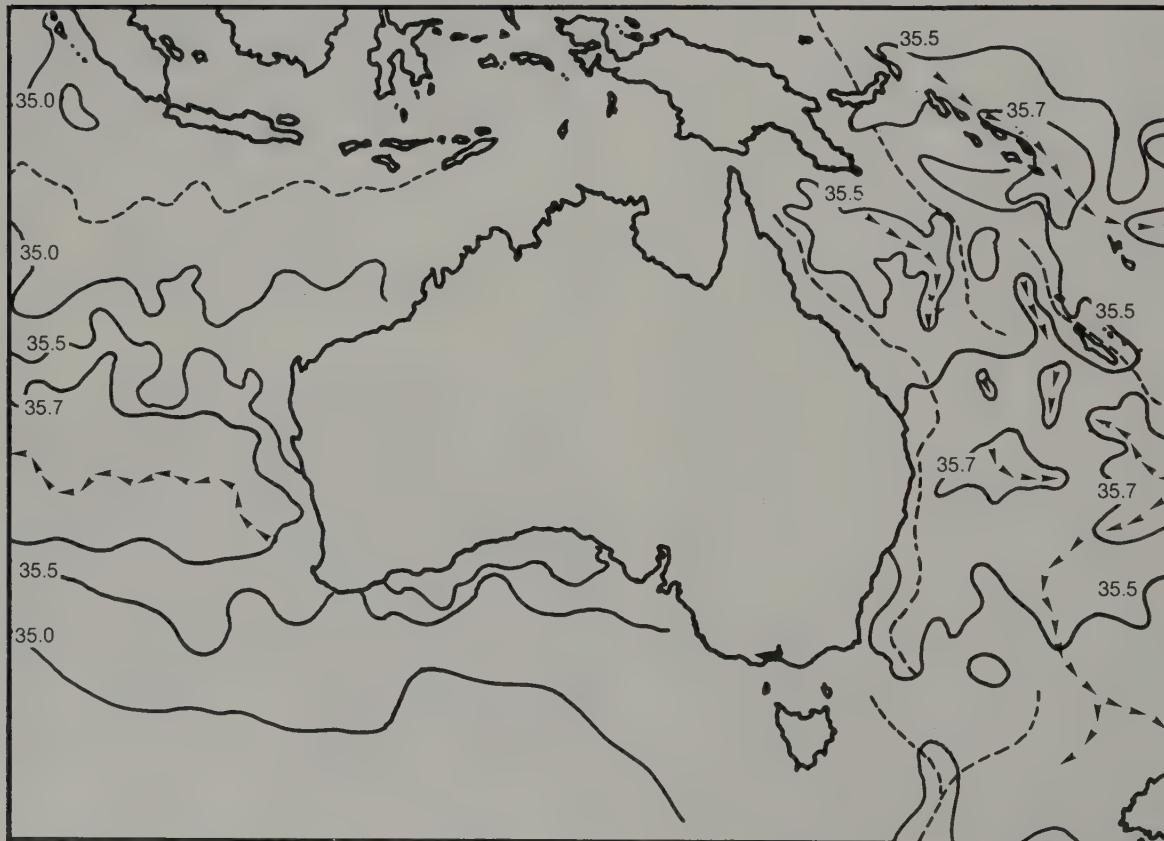


Figure 2.10 The salinity (S‰) at 100 m depth of the oceans around Australia. (After Rochford, 1980)

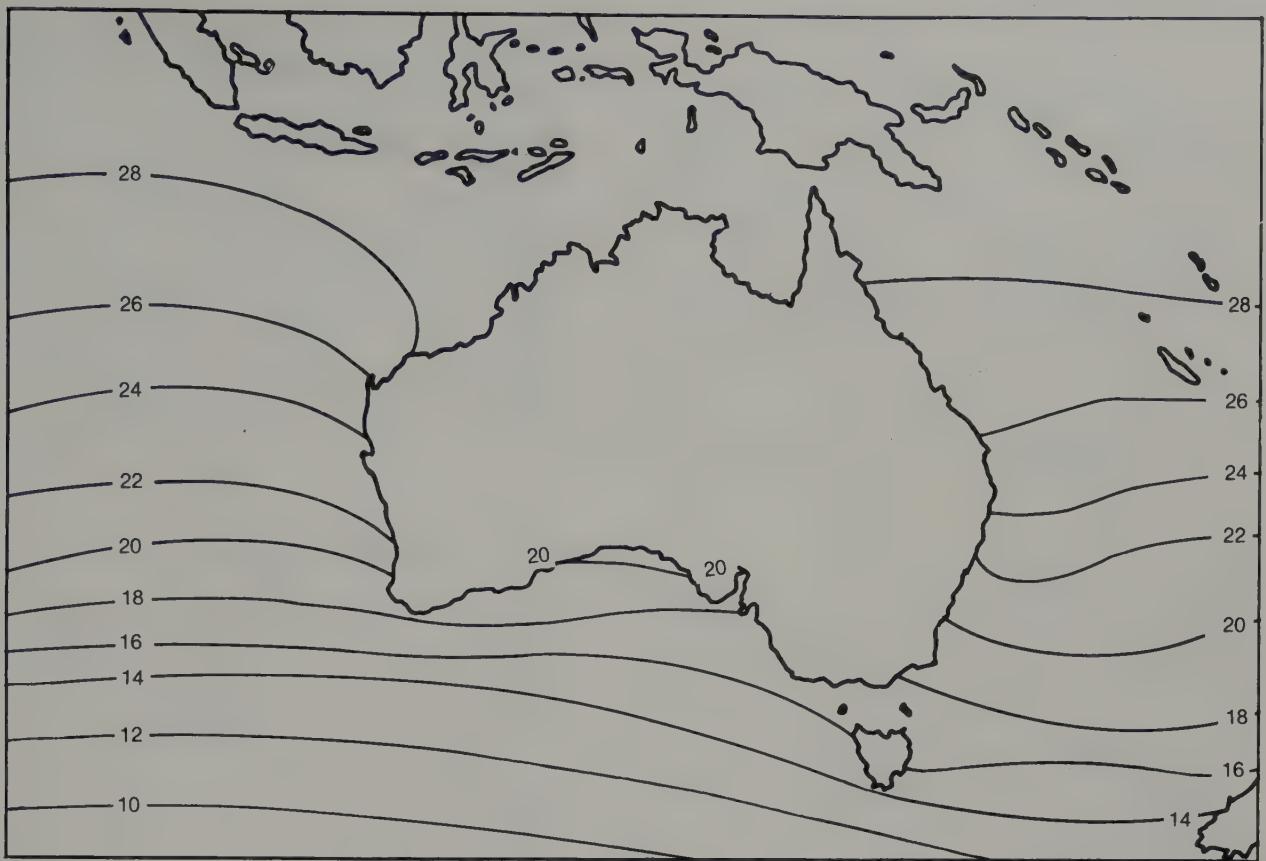


Figure 2.11 The surface isotherms ($^{\circ}\text{C}$) in January in the oceans around Australia. (After Anon., 1981)

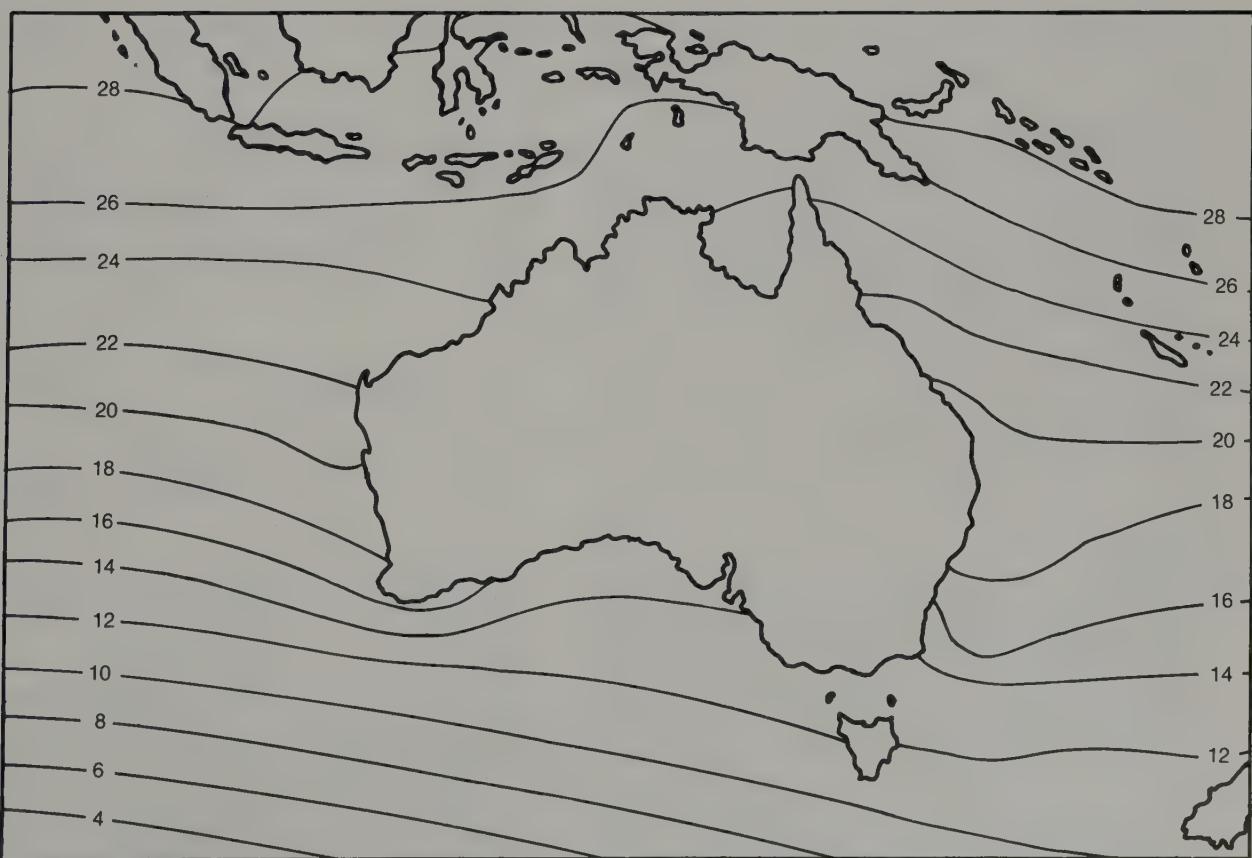


Figure 2.12 The surface isotherms ($^{\circ}\text{C}$) in July in the waters around Australia. (After Anon., 1981)

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Table 2.5 Drainage divisions and their run-off.

DRAINAGE DIVISION AND TYPE	AREA (km ²)	AVERAGE RUNOFF (mill. m ³)
Summer Maximum Rainfall:		
I. Northeast Coast	454 000	82 867
IX. Gulf of Carpentaria	640 800	63 146
VIII. Timor Sea	539 000	74 287
Total	1 633 800	220 300
Mixed Seasonal Rainfall:		
II. Southeast Coast	268 000	36 400
III. Tasmania	68 400	47 171
Total	366 400	83 571
Winter Maximum Rainfall:		
V. South Aust. Gulf	75 370	532
VI. Southwest Coast	140 000	7 223
Total	215 370	7 755
Arid External Rainfall:		
VII. Indian Ocean	520 000	6 160
Total	520 000	6 160
All External Systems	2 705 570	317 786

reveal that deliveries from many Australian watersheds are highly variable and erratic through time. Discharges from the Burdekin River in north Queensland, for example, range over single years from zero to major flood events, whose occurrences coincide with and depend upon the monsoons. In some watersheds, run-off suffers little delay, whilst in others the nature of the substrate and topographic detail, as well as the extent of the catchment, may greatly prolong ultimate discharge. At the other extreme, conditions exist where river flow is perennial. Recorded hydrological variety within estuaries around the coast and within particular ones reflects those influences. Examples include studies by Rochford (1951), Beer & Black (1979), Wolanski (1982) and Messel *et al.* (1981) among many others. Consequences relate to erosion, sediment transport and deposition, patterns and conditions of estuarine inundation, salinity gradients and profiles, water clarity, waterway configuration and a number of other parameters in the physical environment.

Tides

Tidal phenomena are of fundamental importance in the physics of the sea. In the present context, however, tides are of concern because of the periodic inundations they effect at the coast and over other features close to the sea surface. The interaction of tidal flow with discharge from the land is also of interest, but is a subject which has not been widely examined under Australian conditions.

Tidal data for Australia have been taken at standard ports over a number of years and predictions for each are issued annually. A most useful compendium of information on tidal ranges and types has been prepared by Radok (1976), upon which this short account relies. A review by Rossiter (1963) deals concisely with methods of tidal prediction and analysis.

Some of the practical and ecological difficulties associated with obtaining tidal data at locations remote from standard ports and well away from the open sea have been discussed by Bunt *et al.* (1985).

Table 2.6 provides comparative information on tidal range and type from official records for representative locations around the coast. The tabulation reveals only two of many aspects of tidal phenomena, but is useful as a means of reflecting the variety of tidal patterns which exist and also the spread of tidal magnitudes from <2.0 m at Bunbury to around 10 m in the vicinity of Broome. In the parts of Australia where tidal ranges are extreme, coastal gradients are frequently very gentle so that the extent of inundation at the highest tides is considerable. Among other possible consequences, associated high rates of evaporation exert particular influences on estuarine, nearshore and substrate salinities. Steedman (pers. comm.) argues that high salinities developed under those conditions require compensatory mechanisms to maintain balance and suggests that millions of tonnes of salt may be exported from parts of the Western Australia coast each year along bottom haloclines.

Noye *et al.* (1981) should be consulted for details of tidal behaviour in the deep embayment of Spencer Gulf and Church & Forbes (1981) for tidal patterns in the Gulf of Carpentaria. The question of sea-level oscillations imposed over daily tidal records will be considered below.

Wave Climate

There is an extensive literature on this topic, reinforced by engineering interests in beach protection, ports and off-shore structures as well as the studies by coastal geomorphologists. Physical oceanographers are interested in wave phenomena of various kinds, not simply those on the coast and visibly effective at the surface. Waves breaking at shorelines, however, are of particular concern in this account, because of the obvious influence they bring to bear on coastal structures and on the state of the sea as it affects the living environment.

Davies (1977) describes the coast in terms of "process environments" within which he considers wave energy the most important variable. Wave energies around Australia are influenced by continental and regional geography and by climatic variation with latitude. Accordingly, in the southern temperate zone, deep water wave energies are high whereas, in the

Table 2.6 Tidal types and ranges (m) for selected Australian stations. (After Radok, 1976)

LOCATION	TYPE	OBSERVED RANGE (m)
Bamaga, Cape York	Mixed diurnal	3.7
Cooktown	Mixed semidiurnal	3.3
Townsville	Mixed semidiurnal	4.5
Mackay	Mixed semidiurnal	7.0
Brisbane	Mixed semidiurnal	3.0
Sydney	Mixed semidiurnal	2.3
Hobart	Mixed diurnal	2.3
Point Lonsdale	Mixed semidiurnal	2.3
Adelaide	Mixed semidiurnal	4.0
Bunbury	Diurnal	1.8
Carnarvon	Mixed semidiurnal	2.7
Broome	Semidiurnal	10.0
Wyndham	Mixed semidiurnal	8.4
Darwin	Mixed semidiurnal	8.2

north, those energies are generally low. Local or sub-regional conditions, of course, create some variety within each major zone and may, indeed, contribute positively to zone characteristics. For example, the Great Barrier Reef and low offshore gradients, assist in dissipating wave energy, while narrow continental shelves grading steeply to the shore leave the coast virtually without shelter.

The manner in which the wave climate varies through short scales in time and carries its effects to the environment, especially at local scales, is a many-faceted subject that does not lend itself easily to summary. With respect to beach morphodynamics, however, a comparative account for southern Australia by Short & Wright (1984) serves well as an introduction to that field in emphasizing the distinctiveness of the conditions and driving forces. An approach to the engineering perspective, which also has general environmental implications, is provided by Webb (1983).

Water Circulation and Local Topography

This topic is introduced as one of particular interest in relation to the living environment, though little is known about the subject.

On the Great Barrier Reef, circulation and exchange of the overlying waters relate to living communities at a range of scales, some of the larger of which have already been considered. At the scale of individual and within individual reefs, the residence times of the water and the details of its motion, e.g. over reef flats, play a highly significant role in ecological processes, yet little is known of the dynamics involved. Wolanski & Pickard (1983) examine flushing in reef lagoons and Andrews *et al.* (1984) studied stratification in an individual reef lagoonal compartment. At an even more local scale, Andrews & Muller (1983) observed water motions around and through an individual patch reef. The particulars of local topography and the isolated nature of those studies are such that generalizations cannot be made.

The observed departures from mesoscale behaviour are important biologically and demonstrate an outstanding need for information of this kind, whether or not novel physical phenomena are involved. In fact, processes of deep interest not infrequently reveal themselves, as Wolanski *et al.* (1984a) have discovered in investigating wakes and their characteristics in the lee of small islands. The residence times of such structures and the conditions which lead to their decomposition are at once important environmentally and intrinsically interesting.

Small-scale events of many possible kinds have received far too little attention in Australia. Imberger *et al.* (1983), for example, demonstrate the importance of small-scale events, notably in estuaries, and are now carrying their approach to other Australian conditions to understand material fluxes associated with biological productivity.

Extreme Events: Cyclones as a Particular Driving Force

Most, if not all, physical processes in the sea operate at a range of intensities. That variability, as well as frequency distributions in the occurrence and manifestation of particular phenomena, are key elements in signifying environmental quality for living organisms. Those circumstances are well recognized by marine biologists. Comment is limited here, taking tropical cyclones as an example.

Cyclonic events are of particular significance to a large segment of the Australian marine environment. A compendium of information on tropical cyclones in the Australian region

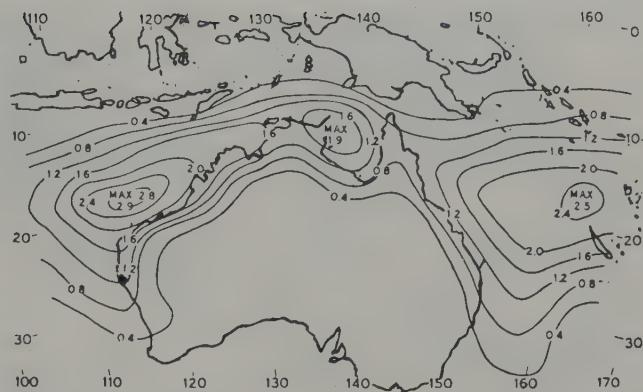


Figure 2.13 Average number of tropical cyclones per year. (After Lee & Neal, 1984)

between 1909 and 1975 was prepared by Lourens (1977). A total of 454 cyclones occurred over the period with an annual average incidence of 9.3. The annual frequency of such events, the tracks followed and their intensities vary widely. Figure 2.13 indicates the distribution of annual frequencies and the broad extent of cyclonic influence.

Lourens (1977) reports that the lowest pressure ever recorded for an Australian cyclone was 914 mb. Even under more moderate conditions, the effects on the sea are considerable. Steedman (1982), emphasizing the need for greater research effort into air-sea interaction associated with cyclones, draws attention to observations off Western Australia which demonstrate cyclones to cause enhanced currents up to 100 cm sec^{-1} up to $>60 \text{ m}$ below the surface, decomposition of stratification in the water column, storm surges, high energy surface waves and long-period waves capable of propagation over length scales $>2,000 \text{ km}$. To these effects, one might add the influence of exceptional precipitation and physical damage to the substrate.

Such effects are dramatic as sources of environmental perturbation. There are, however, many other kinds of extreme events perhaps no less dramatic in effect than cyclones to which the Australian marine environment is exposed. These are often unpredictable and may well be a substantial part of a unique condition. Time-sensitive indicators of general, as well as unusual, events over periods up to 1,000 ybp have now been demonstrated to be preserved in biogenic structures such as corals (Isdale, 1984).

Interstitial Waters

The greater part of this Section has dealt with waters in free motion and, even so, has neglected specific mention of such important topics as the phenomena of mixing. At the same time, there is a need to identify interstitial waters as a distinctive element of the marine environment, as has been done for the sediments with which those waters are associated. Marine interstitial waters have received relatively little attention under Australian conditions. Nonetheless, they are often associated with intense biological activity. This is perhaps most generally recognized by microbiologists and by students of the sea-grasses and mangroves. In mangrove or related intertidal sediments, the most obvious feature of the interstitial waters is their hypersalinity, brought about by processes of evapo-transpiration and direct evaporation at the surface. Elevated salinities are sustained by impeded exchange with adjacent and periodically overlying tidal waters. The mechanisms controlling water movement and exchange through porous media of this kind, however, are not well



Figure 2.14 Inorganic phosphate concentrations ($\text{PO}_4\text{P } \mu\text{g at/L}$) at the surface of the oceans around Australia. (After Rochford, 1980)

understood and the same is true of many other substrates including, for example, reefal carbonates and the diffuse mud-water interfaces so extensive in tropical and other shallow embayments.

THE NUTRIENT RESOURCES AND PHYSICO-CHEMICAL CONDITIONS OF THE MARINE ENVIRONMENT

Baas Becking *et al.* (1960) advance some general propositions about aquatic environments, whether marine or fresh water, which serve as an appropriate introduction to this Section. In essence, they adopt the fundamental parameters of pH and Eh to define aquatic milieux and use thermodynamic considerations to establish the classes of chemical transformations involving living systems that might be anticipated under a variety of pH, Eh conditions. The approach was seen to be relevant primarily at the microbiological level, the foundation of organic fluxes in the sea, and attracted the interest of biological oceanographers such as Wood (1967) in his attention to the microbiology of oceans and estuaries. In particular, Baas Becking *et al.* (1960) undertook to establish what might be termed the boundary conditions of Eh and pH in a variety of environments, including the marine and then identified the boundary conditions for vital processes such as nitrification, denitrification, sulphate reduction and photosynthesis. They conclude that some environments highly restrict biological activity and its diversity while others are far less constraining and that sharp pH and Eh gradients of the kind to be found, for example at mud, water interfaces have great biological significance. The lead offered by those workers, however, has not been widely applied around Australia, although geobiochemical studies in some shallow water and

intertidal situations (e.g. see Boto, 1982; Bauld *et al.*, 1979) represent exceptions. The remainder of the Section will be devoted to nutrient resources about which a good deal of factual information is available.

The primary sources of chemical nutrients to sustain biological productivity in the marine environment are the enriched waters below the thermocline and run-off from the land, as well as nitrogen in combined form derived from the biological fixation of atmospheric nitrogen. Data on nutrient concentrations in the surface waters are normally a reasonable indication of their intrinsic fertility although flux rates from source water masses are the essential determinants of primary productivity. Data on inputs from the land similarly should reflect fluxes. Extensive information exists on concentrations of the major nutrients, N and P, usually measured as NO_3 and inorganic PO_4 , in the Australian sea. Far less data and that of lesser reliability exist on nutrient inputs from the land, either associated with sediments or in solution. The poor N and P status of Australian soils in general limits landward sources except in situations where fertilizer usage is extensive and heavy and leaching is significant (e.g. see Birch, 1982). Such inputs are unlikely, for example, in the series of northern Queensland rivers studied by Boto (pers. comm.) who found inorganic phosphate to lie in the range 0.06 to $0.33 \mu\text{g L}^{-1}$ with nitrate levels generally $<1.0 \mu\text{g L}^{-1}$. Nutrient levels in rivers of the Northern Territory studied by the Department of Transport and Works (pers. comm.) are similarly low.

Insufficient data exist on the nutrient levels of intertidal sediments to permit general assessment, although some information is available for mangrove soils. For example, Boto & Wellington (1983) found ammonium levels between 4.6 and $7.3 \mu\text{g N g}^{-1}$ dry soil and extractable P values from 5.0

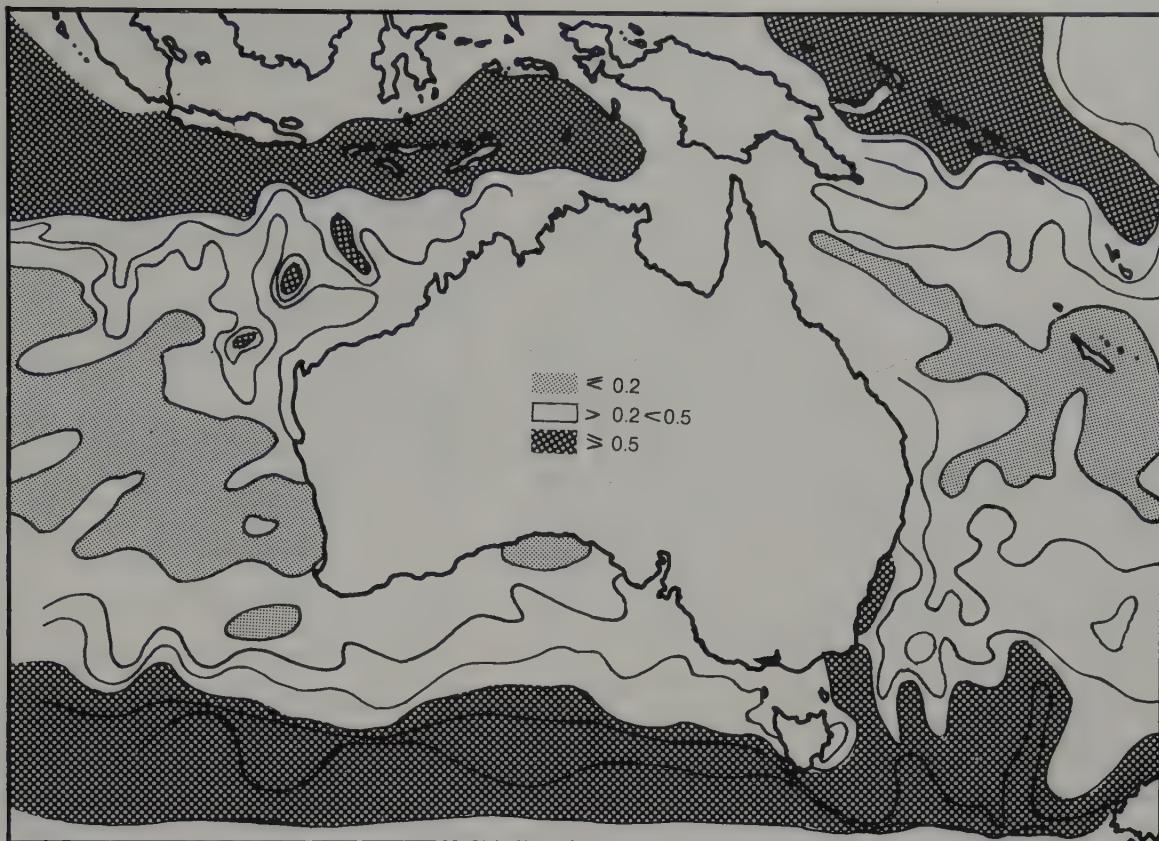


Figure 2.15 The inorganic phosphate concentrations ($\text{PO}_4\text{-P } \mu\text{g at/L}$) at 100 m depth in the oceans around Australia. (After Rochford, 1980)

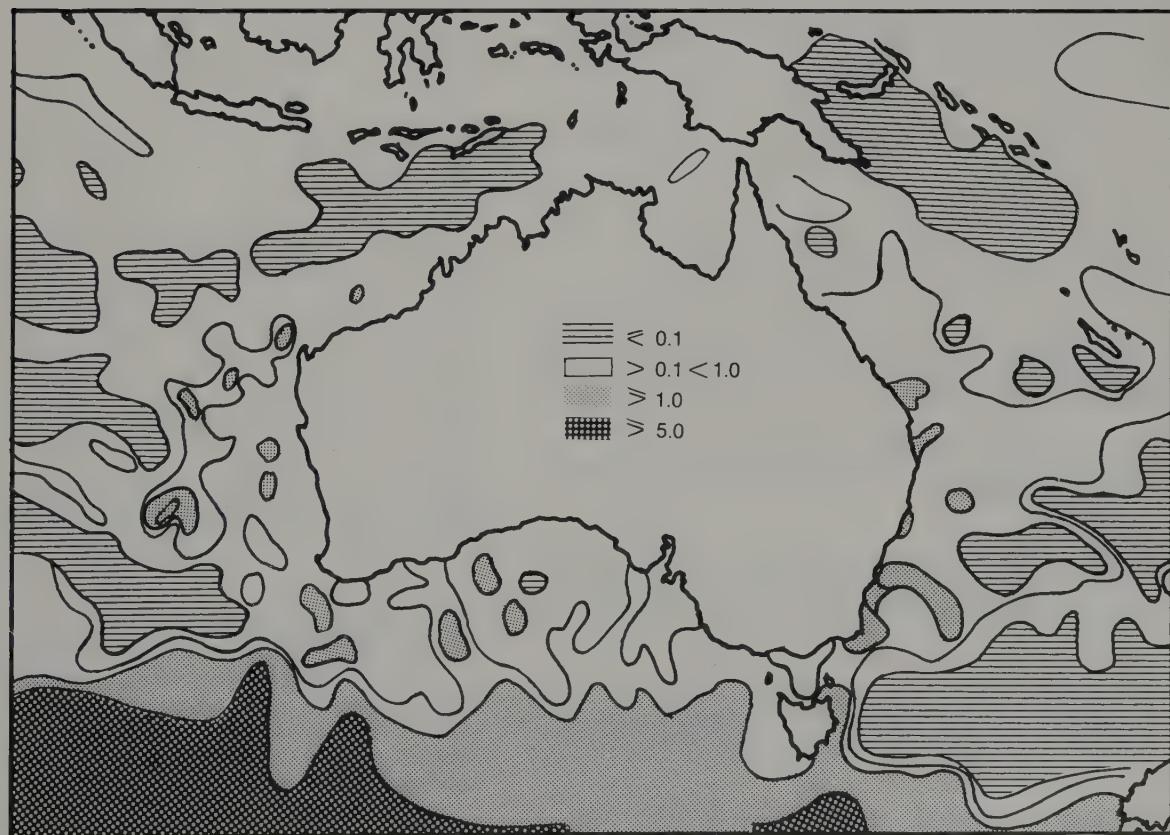


Figure 2.16 The inorganic nitrate concentrations ($\text{NO}_3\text{-N } \mu\text{g at/L}$) at the surface of the oceans around Australia. (After Rochford, 1980)

2. MARINE ENVIRONMENT

to around $20.0 \mu\text{g g}^{-1}$ dry soil at sites in northern Queensland. They were able to demonstrate significant responses in plant growth to fertilizer applications generally for added N and at sites with low P for that element. The extent to which nutrient levels in nearshore sediments are land-derived or sea-derived is uncertain, although concentrations in overlying waters, at least in the tropics, are generally very low. Once again, too little attention has been paid to nutrient fluxes across the land-sea interface to warrant much further discussion.

Even so, various aspects of marine sediment geochemistry have been investigated from the perspective of the geologist and those studies certainly provide information relevant to the understanding of living environments. As an example, Cook & Mayo (1980), in considering the geochemistry of Broad Sound, a tropical estuary, found high phosphate levels in mangrove channels as well as in the interstitial waters where ratios of Mg : Ca were also high. The physico-chemical characteristics and trace element concentrations of the sediments documented so fully would, no doubt, lend themselves to interpretation in the terms suggested by Baas Becking *et al.* (1960). The chemical behaviour of Fe and Mn has been studied in the highly saline groundwaters of a South Australian embayment by Ferguson *et al.* (1983) and Marshall (1983) has investigated the geochemistry of Fe, P, As and Mn in the sediments of the outer continental shelf in New South Wales. Such research is not sufficiently extensive to attempt a synthesis. A "geochemistry of Australian marine sediments" does not exist.

For the Australian sea itself, reference to an overview by Rochford (1980) is essential, since it condenses the work of CSIRO in this field over many years. The results are summarized in Figs 2.14, 2.15 and 2.16, with the distributions of inorganic phosphate at the surface and 100 m and nitrates at the surface for the Australian region. With the exception of certain upwelling areas and south, roughly, of the Subtropical Convergence, the levels of these nutrients are generally low.

With respect to upwellings, Rochford notes nearshore examples off New South Wales at Evans Head and Laurieton, off Victoria near Gippsland and near Port Macdonnell, South Australia. Nutrient enrichment occurs in the warm-core eddies of the southwest Tasman. Higher levels of inorganic PO₄ on the North West Shelf may be the result of upwelling. Enrichment in the eastern Arafura Sea and upper Gulf of Carpentaria appears the result of upwelling off the Aroe Islands. A recent treatment of nitrates in east Australian coastal waters has been given by Rochford (1984). In other recent work on the Great Barrier Reef, Andrews & Gentien (1982) point to the likely significance of upwelling phenomena at the shelf break in carrying nutrients to the reef communities. They estimate an annual input of $20 \mu\text{g N L}^{-1}$ throughout the water column in a 50 km zone in the central province of the Great Barrier Reef. Although there have been many studies of nearshore water fertility at various locations around Australia, the subject has not been reviewed and it would be impracticable to do so here.

FURTHER NEGLECTS

The compilation of an overview of the Australian marine environment is an enormous undertaking and the oversight of some important parameters is inevitable. In that regard, however, I am sensible to the exclusion from the account of climate, an entire subject in itself, but especially of local climate as it relates directly to the intertidal zone and to shallow enclosed waters, of the optical properties of seawater and how that varies, as well as the incoming solar radiation, day length and lunar influences. The living communities themselves have been deliberately set aside to pay attention to the environment; the assumption is that the reader is familiar with the marine biota and that his or her needs might best be served by attempting to draw together information on the surroundings of those organisms and on some of the useful source literature.

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3. MAJOR COMPONENTS AND DISTRIBUTION OF MARINE FAUNA

B. R. WILSON & G. R. ALLEN

INTRODUCTION

The fauna of the coastal waters surrounding the Australian continent, when considered as a single zoogeographic entity, is among the most species-rich and diverse on earth. A combination of factors is responsible for this extraordinary faunal wealth. The most obvious ones are the geographic position encompassing both warm and cool seas, the enormous coastline of great physical diversity and the long history of isolation which has fostered the development of the highly endemic southern temperate fauna.

Australian marine zoologists over the years have been impressed by the obvious fact that species, and to a lesser extent generic distributions, of the marine fauna around the coastline fall into recognizable patterns. Many attempts have been made to classify the coastline into biogeographical provinces based on analyses of these distributional data. Historical and ecological causes for the identified provinces were assumed, but rarely defined. One much quoted representation of reputed Australian marine biogeographical provinces is a figure by Bennett & Pope (1953) reproduced here for historical purposes (Fig. 3.1).

In recent years, a great deal of new information has been gathered on the distribution of living marine species, the biology of many species, past marine faunas, the geological history of the Australian continent and the ocean currents and other physical attributes of the coastal environment. Interpretation of observed distribution patterns in historical and ecological context now may be attempted.

In this account, emphasis is given to the inshore benthic fauna. There is very little information available on the benthic fauna of the continental shelf and beyond. The oceanic pelagic fauna tends to be cosmopolitan and does not exhibit the zoogeographic patterns of the inshore zone.

The general distribution patterns appear to be fundamental. Their origins are in the ancient tectonic events which created and moved the Australian continent to its present position. They are sustained by the modern ocean currents and other physical environmental factors which are themselves products of past events as well as present processes.

GEOLOGICAL HISTORY

The present distribution patterns of molluscs in the Australasian region reflect the interaction of geological, oceanographical and biological events associated with the final breakup of Gondwana and the subsequent dispersion of the continental fragments during the early Cainozoic (Zinsmeister, 1982) and this is probably true of the whole marine fauna.

In the Late Cretaceous there was a broad seaway all around the globe in the equatorial zone and the Atlantic, Pacific and Indian Oceans were continuous in that latitude. That ancient ocean is known as Tethys and, in its shallow parts, it bore a rich tropical marine fauna. The great distance across the

equatorial Pacific may have been a barrier to species dispersal, but the Tethyan faunas of the American and Euro-Asian equatorial regions were essentially the same. At that time, what is now the Australian continent formed a broad end of the Antarctic-Australian shield bulging northward beyond the 60° circle of latitude. There was no seaway between the Southern, Indian and Pacific Oceans (Fig. 3.2).

During the Cretaceous, the high latitude shores of Gondwana, termed the Austral Province by Kauffman (1973), supported many cosmopolitan elements. Fleming (1963) used the term palaeoaustral for groups which were peculiar to that region, derivatives of which still may be recognized in the southern Australian and New Zealand marine faunas. By the Late Cretaceous, according to Zinsmeister (1982), the northern bulge of the Australian end of the then polar East Antarctic-Australian shield caused regional isolation of the southern margin of the Pacific, with the development there of a large endemic component in the marine fauna. This effect would have been emphasized by an ocean circulation pattern in the southern Pacific similar to that of the northern Pacific at present. Zinsmeister (1982) called the region isolated at that time the Weddellian Province. It extended northwards up the coast of Chile and what is now the eastern coast of Australia.

Rifting between the Australian shield and Antarctica began in the Late Cretaceous. By the Eocene, a deep gulf had appeared on the Indian Ocean side which eventually broke through to the Pacific, separating Australia from Antarctica. The Australian Plate began a northward migration. At about the same time, South America lost land connection with Antarctica and Drake Passage opened between the southern Pacific and Atlantic Oceans. Antarctica became isolated at the pole, surrounded entirely by the newly formed circumpolar Southern Ocean (Fig. 3.3).

Opening of the circumpolar Southern Ocean seaway had profound biogeographic consequences. It brought an end to the regional isolation of the Southern Pacific (Weddellian Province) and led to the formation of the Circum-Antarctic Current which, in turn, led to the isolation of polar Antarctica and the deterioration of its climate.

Meanwhile, the rapid northward migration of India and its crash against southern Asia had broken up Tethys. This process was furthered a little later by the closure of the seaway between North and South America and the constriction of the ocean between Africa and Europe to form the almost land-locked Mediterranean of today. The modern Western Pacific and Indian Oceans are the remnant of the once much larger sea of Tethys, together now called the Indo-West Pacific Region.

Impingement of the Australian shield against Southeast Asia partly separated the Indian Ocean from the Western Pacific and incompletely blocked the westward flow of the equatorial currents, but it did not prevent biological connections between them. Instead, it created a wide bridge of shallow sea which became a major centre of speciation and evolution.

3. MARINE COMPONENTS AND DISTRIBUTION



Figure 3.1 Map of the biogeographical provinces of the Australian littoral on exposed coasts. (After Bennett & Pope, 1953)

As late as the Eocene the seas surrounding Antarctica were warm-temperate (Shackleton & Kennett, 1975), but following establishment of the Circum-Antarctic Current, temperature fell rapidly in that region. The modern steep latitudinal sea-temperature gradient and the marked Subtropical and Antarctic Convergences became established in the Southern Hemisphere by the Early Miocene. Although there have been significant oscillations, both in the latitudinal position of the convergences and in sea temperature, the general trend during the second half of the Tertiary has been a temperature fall. Bowler (1982) estimated that sea surface temperatures at 50°S latitude are about 10°C lower today than in the Middle Miocene.

It is these dramatic global tectonic, oceanographic and climatologic events which have shaped the primary distributional patterns of the modern Australian marine fauna.

NORTHERN AUSTRALIA

The modern marine fauna of the vast Indo-West Pacific Region, including northern Australia, is a direct descendant, modified by Tertiary and Pleistocene *in situ* evolution, of the even more extensive Tethyan fauna of the Mesozoic and early Tertiary. The many taxonomic similarities between the modern Indo-West Pacific and Caribbean faunas can be accounted for by common origins prior to fragmentation of the Sea of Tethys.

Today, the Indo-West Pacific Region is incredibly species-rich with a diversity far exceeding that of other tropical regions (Briggs, 1974). It also possesses many endemic genera and families.

An obvious feature of this Region is the high concentration of species in the central part, the triangular area enclosed between the Philippines, Indonesia and New Guinea, which some authors have referred to as the Indo-Malay Archipelago.

The causes of this concentration appear to be the climatic stability of the Region, the extent of shallow shelf areas, the proximity of continental land masses and consequential high productivity and frequency of speciation resulting from

eustatic changes in this geomorphologically complex area. From this centre of high diversity, there is a gradient of decreasing species richness towards the peripheries of the Region.

The northern Australian coast abuts the Indo-West Pacific Region's central high diversity zone. Until the late Pleistocene, the Torres Strait was closed and the northwestern and northeastern coasts were isolated from each other with some degree of endemism in each area as a consequence. The degree of endemism varies from group to group. It is highest in groups such as the volutid gastropods, which have no pelagic larval dispersal stage.

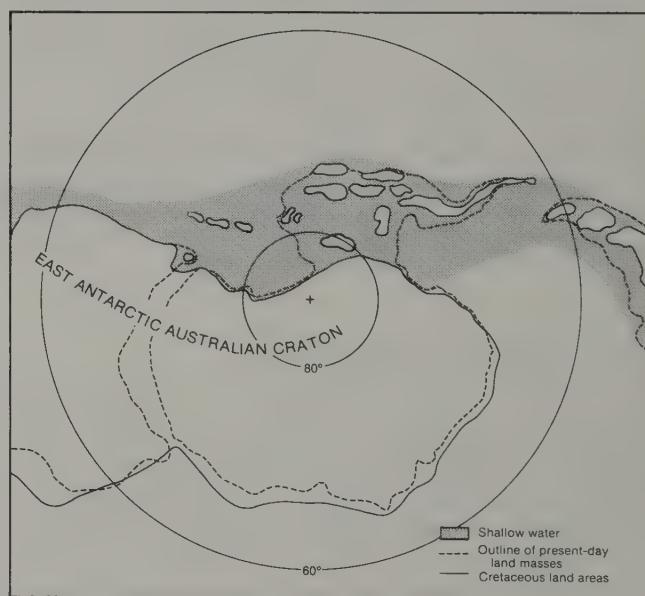


Figure 3.2 Late Cretaceous palaeogeography of the southern Pacific. Stippled area represents inferred areas of shallow marine conditions along the southern margins of the Pacific. (After Zinsmeister, 1982)

SOUTHERN AUSTRALIA

The modern temperate marine fauna of southern Australia has a more complex history and composition than that of the north. For example, apart from a few cosmopolitan elements, the southern Australian molluscan fauna appears to have two major components: one derived from the southern circum-Pacific Palaeoaustral fauna, the other from the tropical Tethyan fauna and, more recently, its Indo-West Pacific descendant.

Palaeoaustral elements have dominated the molluscan fauna of southeastern Australia since the Eocene; a distinct Southeastern Australian Province (Fig. 3.4) may be recognized throughout the middle and late Tertiary (Darragh, 1985). Genera common to southeastern Australia and New Zealand comprised up to 30% of the molluscan fauna in the early Tertiary, as one should expect given the common southern circum-Pacific affinities of these two regions, but the proportion dropped off to 17% by the Pliocene and Pleistocene, presumably as a result of time and divergence in isolation. Another group of genera, those known only from the southeastern Australian region, increased in proportion from 24% of the whole fauna in the late Eocene to 34% in the Pliocene and Pleistocene. Both the Australian-New Zealand and the Australian endemic groups probably have Palaeoaustral origins (Darragh, 1985).

The remaining major component of the Tertiary molluscan fauna of the Southeastern Australian Province was Tethyan or derived directly from the Indo-West Pacific fauna. This element reached its maximum in the mid-Miocene (30% of the genera present *fide*, Darragh, 1985), leading some authors (e.g. Knox, 1980) to suggest that the marine environment there was tropical at that time. The high proportion of northern genera in the Miocene certainly indicates relatively high sea temperature, but whether conditions were actually tropical is doubtful. More likely, the Palaeoaustral fauna and its Tertiary southeastern Australian and modern southern Australian derivatives, have always been a temperate assemblage.

From the Miocene to the early Pleistocene, the Southeastern Australian Province was confined to the extreme southeastern corner of the continent where its fauna is represented in the fossiliferous sediments of the Gippsland, Bass, Otway and Murray Basins but not further west (Fig. 3.4). Throughout that period, the western part of the southern Australian coast was dominated by Tethyan and Indo-West Pacific elements. This area is regarded as having been an arm of the Indo-West Pacific Region through the Miocene to early Pleistocene period, called the Austral Indo-Pacific Province (Crespin, 1950; Ludbrook, 1954; 1969; Darragh, 1985). There is little doubt that it supported a tropical or subtropical fauna, now represented in the richly fossiliferous sediments of the Eucla and St Vincent Basins in Western and South Australia. Examples of ancient and once wide-spread Tethyan elements in the molluscan fauna of the Austral Indo-Pacific Province are the gastropods *Campanile* and *Diastoma*, each of which has a single relict species still surviving in the southwest, and the bivalve *Miltha* which is now extinct in Australia and the Indo-West Pacific, but survives in tropical waters of Baja California and Brazil.

Modern Indo-West Pacific molluscan genera in the Pliocene and early Pleistocene of the Austral Indo-Pacific Province are legion, examples being the bivalves *Pinctada*, *Anodonta*, *Cucullaea* and *Timoclea* (*Vermolpa*) and the gastropods *Chicoreus*, *Haustellum*, *Homolocantha* and *Tudicula*. There is a number of examples of species which are present in the Eucla Basin as late as the early Pleistocene, but which have now retracted to the west or northwest coast of Western Australia, for example *Amoria grayi*, *Angaria torah*, *Cymbiola* (*Aulicina*) *irvinae* (Ludbrook, 1978).

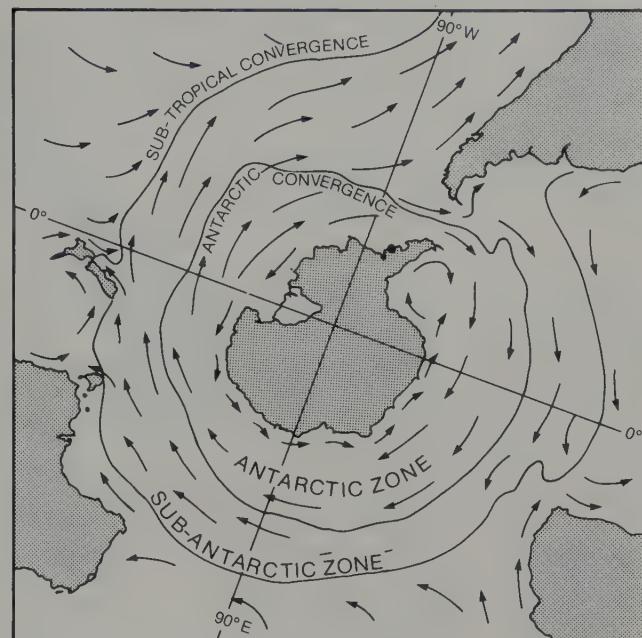


Figure 3.3 The Southern Ocean with the mean position of the Antarctic and Subtropical Convergences and the principal surface water movements. (After Knox, 1979)

The Cainozoic fossil mollusc fauna of southern Australia thus reveals a history of fluctuating influence and interaction between two major marine faunas following the Eocene creation of the southern Australian coast, one pushing westwards from the southern Pacific and the other pushing eastwards from the Indian Ocean. Since the beginning of this process, the extreme southeastern corner of Australia has been the bastion of a marine fauna which had its origins in the cooler waters of the southern Pacific in the Late Creta-

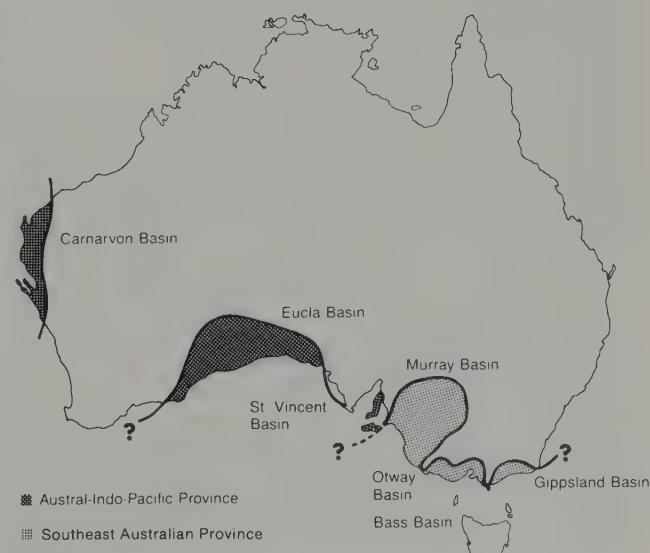


Figure 3.4 Southern Australian Tertiary marine basins and the marine faunal provinces to which they are assigned. Tertiary marine basins occur between the late Early Miocene and the Pleistocene. (After Darragh, 1985)

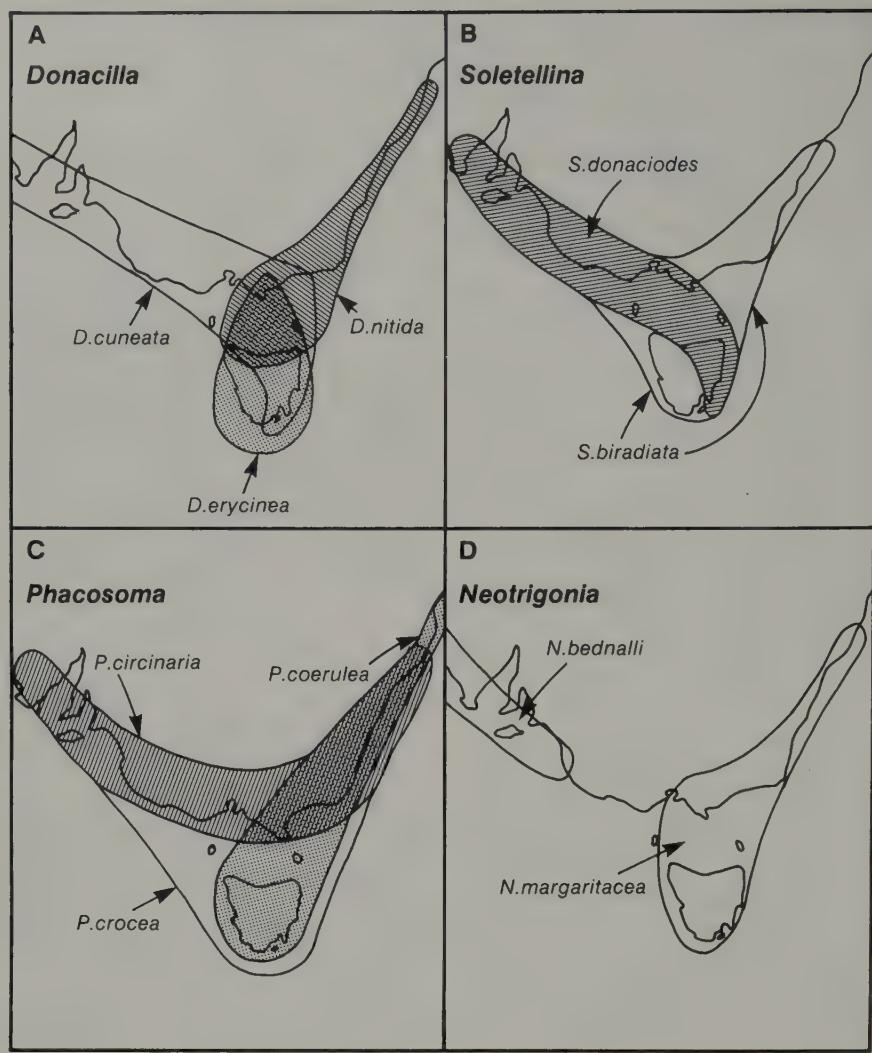


Figure 3.5 Distribution patterns of nine species of bivalve molluscs in southeastern Australia. (After Dartnall, 1974)

ceous and early Tertiary. Much of the high degree of endemism evident today in the southern Australian fauna has those southern Pacific origins.

The strong push of tropical elements from the west (and possibly also from the north down the eastern coast) which peaked in the Miocene, but continued until the early Pleistocene at the head of the Great Australian Bight (Roe Plain), eventually failed, presumably due to a general fall of sea-temperature and associated changes in oceanographic conditions. Relicts of these tropical Tethyan and more modern Indo-West Pacific elements remain, especially in the southwest. Nevertheless, the peculiar modern temperate marine fauna of the southern coast of Australia is derived largely from a Pleistocene expansion of the Tertiary Southeastern Australian Province (Darragh, 1985).

During the Pleistocene, a further complication was the dramatic fluctuation in sea-level which, at times of low sea-level, kept Bass Straight dry, separating the western and extreme southeastern parts of the temperate southern coast. The evolutionary results of this can be seen today in the distribution of many species and subspecies pairs in the region. In some cases, the eastern and western daughter species, which evolved during periods of isolation, remain allopatric (Fig. 3.5D). In others, the daughter species re-established zones of overlap or sympatry in Bass Strait after it was re-flooded (Fig. 3.5A,B,C).

EFFECTS OF OCEAN CURRENTS

The preceding Section gives an account of the geological history of the Australian marine fauna which emphasizes the dynamism of coastal species' distribution patterns over large time spans due to the interactions of changing environmental conditions, spatial relations of land masses and evolution. Environmental changes commonly are discussed only in terms of temperature. Ocean currents, however, are another important factor, providing the mechanism aiding (or inhibiting) expansion or maintenance of range, at least for those species with pelagic larval dispersal capacity. Ocean currents, too, are subject to change as land masses alter position and global climates change. They also may vary seasonally, rendering ends of the range of some species unstable. Long term and short term effects of ocean currents are evident on Australian marine fauna distribution patterns.

An account of the currents presently around Australia has been given elsewhere (Chapter 2). Several features are noteworthy in the context of this Section.

South Equatorial Current

The westward flow of this current in the western Pacific is dispersed when it meets New Guinea and northeastern Australia. An arm of it turns southwards and becomes the East

3. MARINE COMPONENTS AND DISTRIBUTION

Australia Current. A significant component pushes through Torres Strait and flows across northern Australia into the Arafura Sea. Other components pass around the northern side of New Guinea and between the eastern islands of Indonesia into the Timor Sea. In that area, the Indian Ocean part of the current is reconstituted and continues its westward flow across the Indian Ocean.

The biogeographic consequences of this current are several. It accounts for the strong Pacific element in the coral reef fauna of the shelf-break atolls (Seringapatam, Scott Reef and the Rowley Shoals) on the North West Shelf (Wilson, 1985a). A similar Pacific influence on the marine fauna of Cocos-Keeling Atoll presumably has the same cause.

Westward flow of the South Equatorial Current through Torres Strait may enhance transport of eastern Australian species in that direction, but inhibits larval transport in the other. There is insufficient knowledge about species distribution in northern Australia to demonstrate this effect, but a physical bottleneck of this kind at Torres Strait does support the likelihood of a dispersal barrier at that point.

Finally, the build-up of Pacific throughflow in the Arafura and Timor Seas is enhanced in winter by the effects of the southeastern trade winds. The winds appear to provide the driving force for a longshore current southwestwards down the North West Shelf and the origins of the Leeuwin Current.

East Australia Current

The arm of the South Equatorial Current which turns southward down the northeastern coast of Australia, forms the warm episodic, southwestern Pacific boundary current known as the East Australia Current.

At the surface near the shelf edge, it flows at rates up to 2 m sec⁻¹ (Hamon *et al.*, 1975). At about 33°S, the current veers away from the coast and flows southeasterly across the north end of the Tasman Sea (Boland & Church, 1981). The latitude where this occurs varies. On some occasions, a U-shaped warm tongue extends further south along the coast of New South Wales as far as Sydney or beyond. Once or several times each year the southerly end of this tongue is pinched off to form anticyclonic whirlpools which may meander erratically in the western Tasman Sea. These vast lenses of slowly spinning water are known as "warm-core eddies". They may survive as identifiable water masses for up to two years.

The East Australia Current provides a mechanism for the dispersal of pelagic larvae from north to south along the coast of Queensland and the northern coast of New South Wales. The extent of its southerly penetration varies from year to year. Over an extended time scale, this current could have been responsible for invasion of tropical Indo-West Pacific species into southeastern Australian waters.

The warm-core eddies are extraordinary structures which transport and maintain tropical Coral Sea nektonic and planktonic organisms within their warm water masses far south into the temperate zone of the Tasman Sea (Wadley & Lu, 1983). They also are a potential source of tropical migrants into the temperate zone and complicate distribution patterns of the southeastern Australian off-shore fauna.

Leeuwin Current

Unlike other continental western coasts, the western coast of Australia is served by a fast, southward flowing offshore current, recently discovered and known as the Leeuwin Current (Fig. 3.6). It is seasonal, flowing most strongly in au-

tumn and winter at rates of as much as one metre per second. Originating off North West Cape, the Leeuwin Current is a narrow tongue of warm, low-salinity water which travels along the shelf-break to Cape Leeuwin before turning eastwards and ending in a slowly turning knot of whirlpools in the Great Australian Bight (Pearce & Cresswell, 1985). Although the southerly autumn-winter flow of the Leeuwin Current is strong and well defined, in summer it is relatively weak and irregular.

The zoogeographic significance of this remarkable current is profound. It accounts for many extraordinary distributional patterns evident in the Western Australian marine fauna. The existence of the Abrolhos coral reefs in latitude 29° far south of the usual coral reef zone, is undoubtedly due to the warm water and pelagic larval recruits carried southwards by the Leeuwin Current. The recent discovery of mass autumn spawning of corals on the northwestern coast (C. Simpson, pers. comm.), at the season when the Leeuwin Current flows most strongly, supports that conclusion. The occurrence of many tropical intertidal animals at Rottnest Island and further south along the Naturaliste-Leeuwin coast, and even further along the southern coast of Western Australia, also may be attributed to the effects of this current.

Benthic dredging cruises by the Western Australian Museum between Shark Bay and Cape Leeuwin revealed the presence of several tropical shallow water gastropods (such as *Chicoreus cervicornis*), otherwise found only north of North West Cape, on the outer shelf as far south as Cape Leeuwin (Wilson, unpubl. data). This observation may also be explained by the Leeuwin Current which is narrow but deep, intersecting the sea-bed at the outer edge of the shelf (Fig. 3.7).

Maxwell & Cresswell (1981) draw attention to the dispersal of tropical marine fauna to the Great Australian Bight by the Leeuwin Current. One may easily suppose that this mechanism is of long-standing (though possibly inconsistent) and that it was the mechanism in the latter half of the Tertiary which established the tropical Austral Indo-Pacific Province along the western part of the southern Australian coast. A small increase in the strength of the Leeuwin Current, especially in summer, might be quite enough to create warm conditions and to populate the Bight with a tropical Indo-West Pacific fauna like the one which flourished there (*i.e.* Roe Plain) in the early Pleistocene. The eastward limit of this current's influence, likely to be in the eastern part of the Bight in those circumstances, may have been the "barrier east of Kangaroo Island which filtered" Indo-Pacific immigrants to the Southeastern Australian Province postulated by Daragh (1985). Conversely, the westward contraction of the Indo-West Pacific fauna in the Bight after the early Pleistocene, and the westward expansion of the Southeastern Australian Province to fill the gap, may have been due to a decrease in strength of the Leeuwin Current as well as a general fall in sea temperature.

Godfrey & Ridgway (1984) argue that outpouring of water from the Pacific Ocean into the Timor and Arafura Seas through deep channels between the Indonesian islands establishes a longshore pressure gradient down the Western Australian coast, creating the primary force which drives the Leeuwin Current. The current literally runs down hill. If this is true, one may suppose that this circumstance was initiated when the Australian plate impinged upon that of southeastern Asia. This tectonic event, therefore, may have created not only the southern Australian shore, but an oceanographic mechanism which pumped in warm water and Indo-Pacific fauna to populate it.

The strength of the Leeuwin Current may have been influenced by the effects that eustatic change in the northern Australian-Indonesian region must have had on the amount

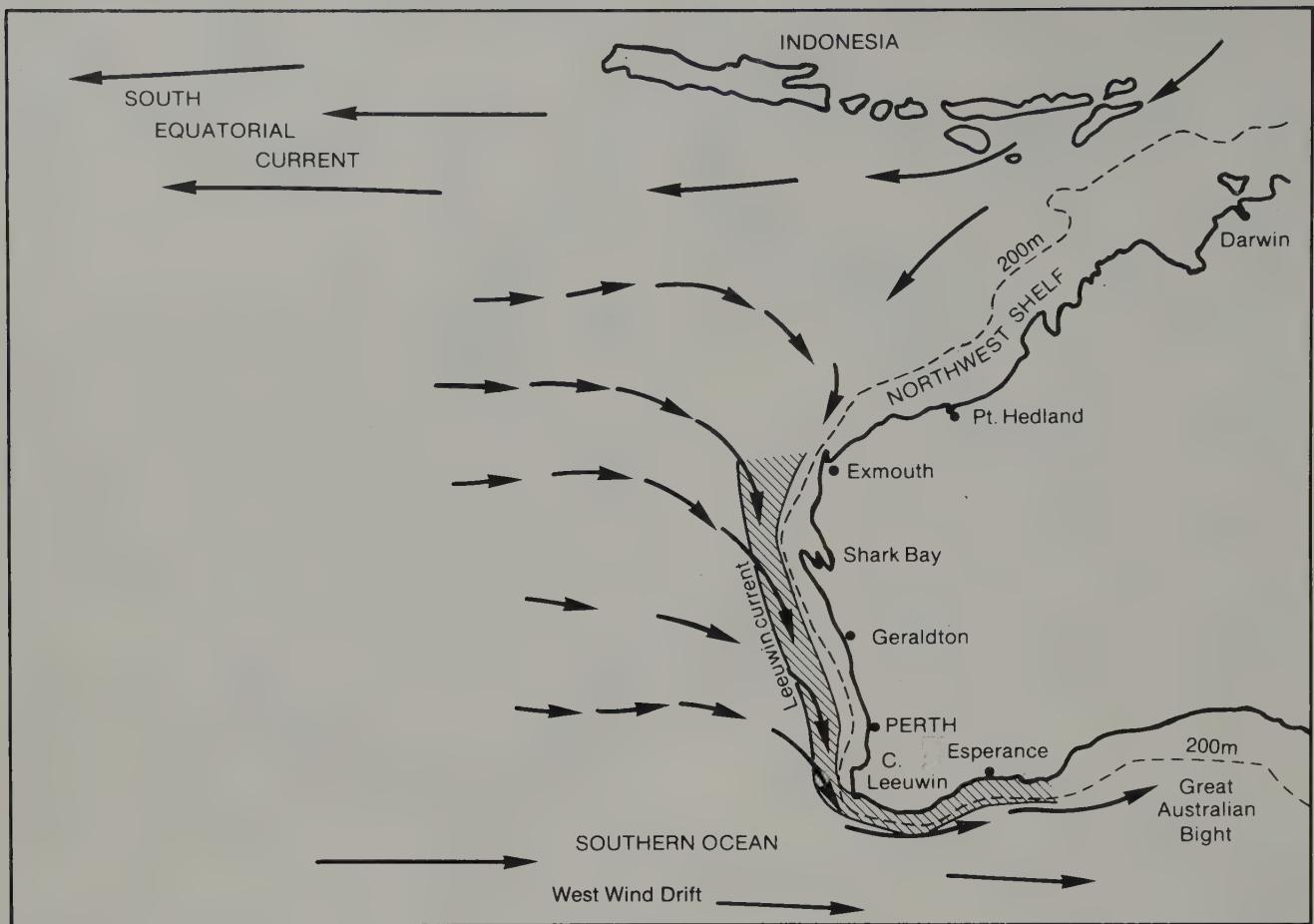


Figure 3.6 Schematic chart of mean large-scale circulation in the eastern Indian Ocean showing the Leeuwin Current and the West Wind Drift.
(Modified after Pearce & Cresswell, 1985)

of water flowing in from the Pacific. During Pleistocene glacial periods of low sea-level (and low temperature), flow through the Torres Strait mostlikely was restricted or lacking and the Leeuwin Current weak or absent.

The previously mentioned early Pleistocene tropical fauna in the Great Australian Bight may represent a period of maximum flow. Conversely, Pleistocene guano deposits at the Houtman Abrolhos Islands seem strong evidence of one or more periods when local up-welling occurred in that region, which in turn implies failure of the Leeuwin Current and the temporary development of a northward flowing boundary current in the eastern Indian Ocean. Certainly, at least during the Pleistocene, successive changes in the strength of the Leeuwin Current caused the interface between the Indo-West Pacific and southern Australian faunas to oscillate around the western and southwestern coasts of Western Australia. Pivotal points in this dynamic interaction between the two distinctive faunas appear to be North West Cape and Cape Leeuwin.

West Wind Drift

Creation of the Southern Ocean in the early to middle Tertiary established circumpolar currents in southern high latitudes, one of which, the West Wind Drift, flows across the southern face of Australia at the present time. The latitudinal position of this current varies seasonally.

In the far west, the West Wind Drift passes to the south of Cape Leeuwin. Generally, it flows beyond the shelf edge, but periodically it intrudes into the shelf break, especially when the Leeuwin Current is weakly developed. There are few data concerning this current in southern Australian waters, but it seems likely that it impinges most strongly on Bass Strait and the west coast of Tasmania. It may be responsible for observed winter intrusion of cold water into the Tasman Sea through the Bass Strait (Gibbs *et al.*, 1976). That intrusion curls northward up the eastern coast of Australia and may be the mechanism for transport of southeastern Australian fauna up the coast of New South Wales, counter to the southerly flow of the East Australia Current.

The West Wind Drift is responsible for the transport of cool-temperate "cosmopolitan" elements into the southern Australian marine fauna. Such species necessarily have long-lived pelagic larval stages or epipelagic adults and they or their close relatives tend to occur in southern Australia, New Zealand, Chile, South Africa and the sub-Antarctic islands (Knox, 1963; 1979; Edgar, 1986). Examples include the Southern Rock-lobster, *Jasus lalandii* and the Blue-mussel *Mytilus edulis*. The latter species has a similar circumpolar distribution in the Northern Hemisphere, so that it is circumpolar and bi-polar in distribution. Fell (1962) discussed the distribution of Southern Hemisphere echinoderms which have a high latitude circumpolar distribution (for example *Patiriella*), emphasizing the characteristic eastward dispersal of these groups. This cool-temperate element has been an important component of the marine fauna of southern Australia since the middle Tertiary.

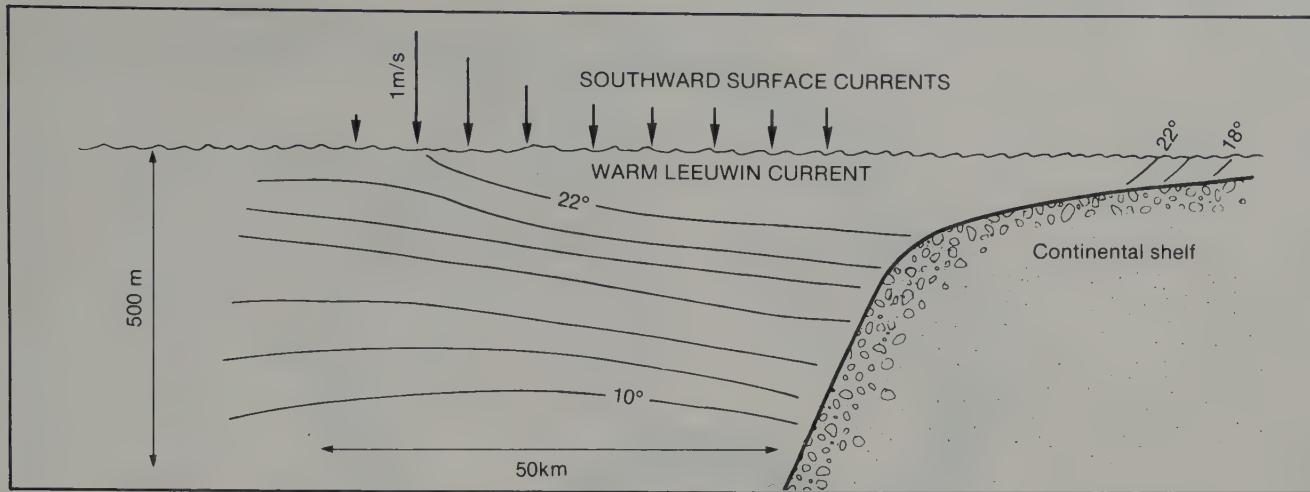


Figure 3.7 Schematic horizontal profiles of surface current, temperature and salinity across the Leeuwin Current. (After Pearce & Cresswell, 1985)

DISTRIBUTION PATTERNS OF THE MODERN MARINE FAUNA

In this Section, distribution patterns for Australian fishes, molluscs, echinoderms and corals are reassessed and interpreted in historical and ecological contexts. These groups have been selected because the taxonomy and distributions of their taxa are now relatively well known and because they elucidate general principles which may apply to the marine fauna as a whole. The molluscs are particularly useful because of their excellent and informative fossil record in southern Australia.

The most striking feature of the Australian marine fauna is that it consists essentially of two very distinct latitudinal elements separated by zones of inter-mixing. Wilson (1971) referred to these as the faunas of the Northern Australian Region, the Southern Australian Region and the Eastern and Western Overlap (transition) Zones on either side of the continent (Fig. 3.8).

Broadly speaking, northern Australia is part of the tropical Indo-West Pacific Faunal Region. It has an extremely high species diversity and the majority of these species are distributed widely in the tropical Indian and Western Pacific Oceans. There is some Australian endemicity, however, and there are some differences between the faunas of the northwestern and northeastern coasts. In contrast, the marine fauna of temperate southern Australia is characterized by lower diversity and very high species endemicity. The eastern and western overlap zones are long stretches of coastline between the northern and southern regions where, in broad terms, there is a gradual replacement of tropical forms with temperate ones as well as some local endemism.

FISHES

Based on a recent synopsis of Paxton *et al.* (in press and in prep.) the Australian fish fauna is estimated to contain about 3,600 species (Table 3.1). Approximately 700 of these are offshore forms which occupy deep benthic habitats (below 200 m) or live in the midwater or pelagic realm. The offshore benthic fauna is poorly known, largely due to inadequate sampling.

Midwater and pelagic fishes, which sometimes are important commercially, are generally widespread. Many of them are

migratory, especially tropical species which visit cooler southern waters during summer. The billfishes (Istiophoridae and Xiphidae), for example, often migrate southward where food is more abundant during summer and then back to tropical waters for spawning or over-wintering. The Black Marlin (*Makaira indica*) is a well-known visitor to the Great Barrier Reef near Cairns. The marlin congregate in the northwestern Coral Sea to spawn between October and December. Similarly, the Blue Marlin (*Makaira mazara*) is a summer visitor off Rottnest Island, near Perth and has been taken as far south as Albany. Presumably, they migrate from tropical latitudes in search of food such as tuna, skipjack, wahoo and dolphinfishes. Less well known are the migrations of flying fishes (Exocoetidae), which are abundant in tropical seas, but extend their range southward during summer.

Some fishes appear to make use of ocean currents as "a conduit to other areas" (Cresswell, 1986) in the course of their seasonal migrations. The Australian Salmon (*Arripis trutta*) and the Southern Bluefin Tuna (*Thunnus maccoyii*) may be "riders of the Leeuwin Current" by which they travel across the southern coastline after their annual spawning off the southwest coast.

Little is known of the migratory pathways and distribution patterns of pelagic fishes. The present discussion is confined mainly to the approximately 2,500 species of inshore fishes which occupy a variety of marine and estuarine habitats to depths of 200 m or roughly the edge of the continental shelf.

Several biologists, beginning with Hedley (1926), have proposed zoogeographic regions or provinces to accommodate the Australian fish fauna. Ichthyologists frequently refer to Whitley's (1932) scheme (Fig. 3.9), a refinement of Hedley's work. Recent developments have enabled a fresh zoogeographic analysis of fish distribution patterns to be undertaken. Firstly, recent in-depth systematic revisions of important families have been completed or are presently being undertaken by both Australian and overseas workers. These include reviews of shark families (Compagno, 1984), Antennariidae (Pietsch, 1984), Atherinidae (Ivantsoff, 1978), Syngnathidae (Dawson, 1985), Hemiramphidae (Collette, 1974), Lutjanidae (Allen, 1985), Chaetodontidae and Pomacanthidae (Steene, 1978; Burgess, 1978; Allen, 1979); Pomacentridae (Allen, 1975 and in progress), Blenniidae (Smith-Vaniz, 1976) and Scombridae (Collette & Nauen, 1983). Important revisionary works are in progress currently

3. MARINE COMPONENTS AND DISTRIBUTION

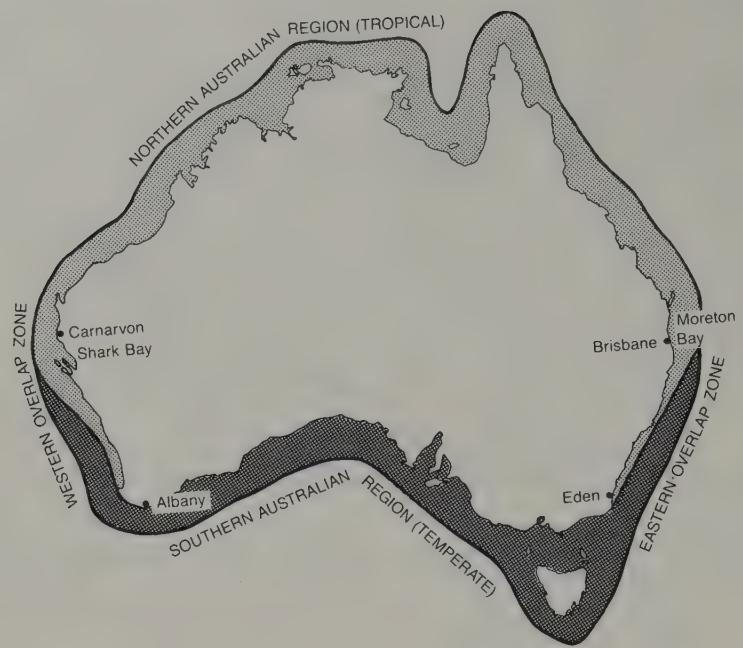


Figure 3.8 Major faunal regions of the Australian coast. (After Wilson, 1971: Fig 10)

on other groups and the authors have been fortunate in being provided access to these unpublished data. The partially completed checklist of Australian fishes by Paxton *et al.*, which will be published by the Australian Biological Resources Study as part of the *Zoological Catalogue of Australia*, has been particularly helpful. This compilation of the Australian fauna draws on the work of numerous specialists. Another important source is the work of J.B. Hutchins of the Western Australian Museum who has made a series of comprehensive reef fish collections around the southern coast and is currently preparing a paper on the zoogeography of the temperate fish fauna.

Major Zoogeographic Zones

Northern Tropical Zone: The extensive tropical zone (Fig. 3.8) contains the bulk of the Australian inshore fauna with an estimated 1,900 species and 600 genera belonging to about 120 families. The majority of species is shared with adjacent regions in the vast Indo-West Pacific Province. Many of these are distributed from East Africa to the islands of central Oceania. Fishes found on or in the vicinity of coral reefs are by far the dominant element of the northern fauna, but there are also many species found in relatively turbid nearshore habitats and estuaries.

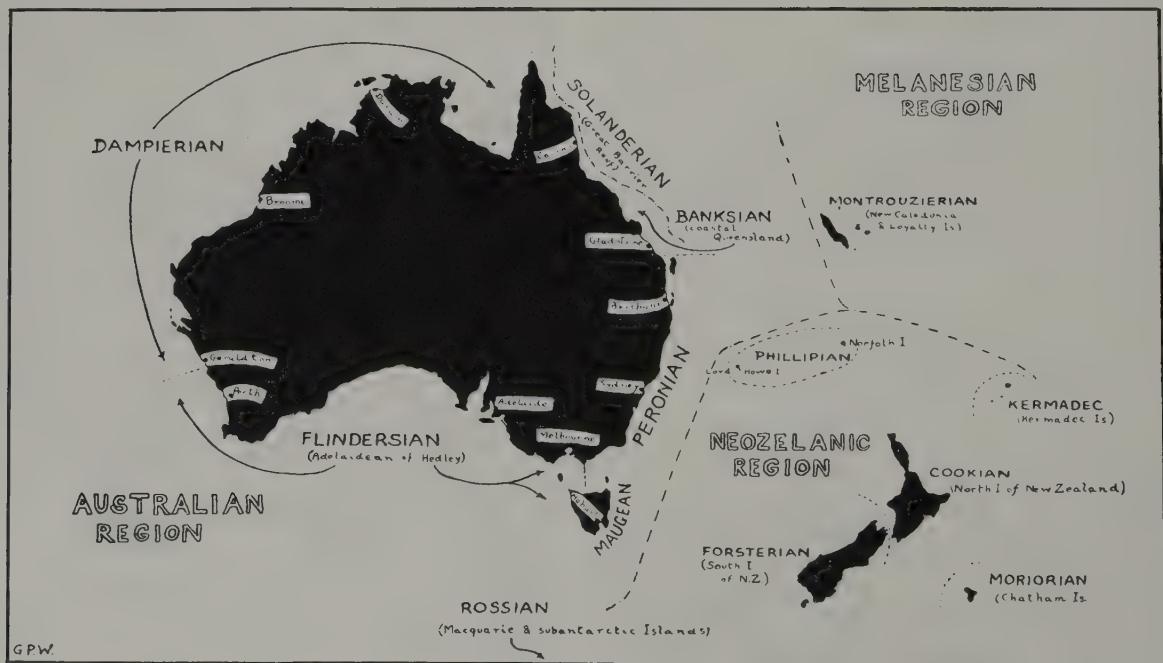


Figure 3.9 Zoogeographic Regions of Australia as proposed by Whitley 1937.

3. MARINE COMPONENTS AND DISTRIBUTION

The eastern coast of Queensland is the most species-rich region within the tropical zone, reflecting the extensive coral reef habitat, complemented by well-developed nearshore and estuarine faunas.

The northern section, between Cape York and North West Cape, has a comparatively impoverished fauna due to the poor development of coral reefs. The area is characterized by huge tides, discharge from large, muddy rivers and extensive mangrove habitat. The relative poverty of the northwest is apparent if the fish faunas of Lizard Island on the Great Barrier Reef and North West Cape, Western Australia are compared. Surveys have yielded about 800 and 460 species from these respective localities (Table 3.2). A similar discrepancy has been noted between the Barrier Reef and the coral atolls lying near the edge of the North West Shelf (for example Rowley Shoals and Scott Reef).

There is a significant endemic element in the northern fauna, with about 13% of the species and 9% of the genera in this category. Of these, about 40% are restricted to the eastern coast and Great Barrier Reef, 30% are from seas west of Cape York and 30% have widespread distributions encompassing both of these regions.

Most of the endemic genera (Table 3.3) are monotypic and are members of relatively large families that are distributed throughout the tropical Indo-West Pacific. There are three endemic families in the region, which includes New Guinea, all of which are monotypic (Table 3.4).

The combination of pelagic egg and larval stages possessed by the majority of tropical reef species is evidence of their dispersal ability. Larval transport by currents from adjacent regions, particularly the Indo-Malaysian and Melanesian archipelagos to the north, no doubt contributes to recruitment into northern Australian populations of widespread Indo-West Pacific species. Unfortunately, there is insufficient phylogenetic information pertaining to tropical Australian fishes to permit reconstruction of the sequence of events which led to the speciation of the endemic forms. Certainly, the intermittent Pleistocene land bridges across Torres Strait have contributed to the process. The integrity of the Australian endemic populations is no doubt enhanced by the southerly flowing currents on both sides of the continent.

Southern Temperate Zone: In contrast to the northern fauna, the fishes of southern Australian temperate seas are highly endemic at the specific and generic levels. Of the estimated 600 inshore species, about 85% are endemics, while 11% are shared with New Zealand. The remaining 4% are circumtemperate and circum-Australian species or are shared with other southern continents. Endemism at the generic level is about 38% (of the estimated 290 genera).

The general composition of the southern fauna at the family level is much the same as other warm temperate regions. Only six families containing 13 species and seven genera are endemic (Table 3.4). A number of families, however, have undergone radiation that is unparalleled elsewhere. This phenomenon is particularly apparent in a number of families that normally have their main strength in tropical waters of the Indo-Pacific, for example Antennariidae, Syngnathidae, Serranidae, Labridae, Gobiidae, Monacanthidae and Tetraodontidae. Some of these radiations probably originated from Tethyan ancestral stock. The radiation of these forms may have been enhanced in cooler, southern seas due to reduced species diversity compared to the tropics. In other words, the temperate environment would appear to offer more opportunities for niche specialization because of lowered competition.

Interestingly, the four families exhibiting the most speciation (Table 3.5) are characterized by reproductive modes that tend to discourage extensive dispersal. Clinids are viviparous; syngnathids are pouch brooders and both gobiesocids and

Table 3.1 Summary of the Australian fish fauna.

MAJOR CATEGORY	ESTIMATED NO. SPECIES
Tropical, inshore, marine	2 000
Midwater, pelagic, deepsea	700
Temperate, inshore, marine	600
Freshwater	180
Awaiting description (in museum collections)	120
Total	3 600

gobiids tend demersal nests, although they have pelagic larval stages of undetermined duration. These groups appear to have been particularly susceptible to explosive radiation in response to the southern dispersal barriers that are discussed below.

Three families that are particularly noteworthy for their explosive radiations in Australia are the pipefishes and seahorses (Syngnathidae), leatherjackets (Monacanthidae) and anglerfishes (Antennariidae). According to Dawson (1985), "the Australian pipefish fauna is unique in its diversity and exhibits a high degree of endemism". Nearly 80% of the 47 genera in the Indo-Pacific region (including the eastern Pacific) are represented in Australia and 14 (38%) of these are endemic, including 10 which are monotypic. Five areas of regional endemism are recognized (Dawson, 1985): the northeast from Torres Strait south to Sandy Cape (24°36'S) with 45% endemism; the southeast from Sandy Cape to about Bermagui, New South Wales (36°25'S) with 26%; the southern region from Bermagui to Robe, South Australia (139°45'E), including Tasmania, with 17% and the southwest from Robe to Shark Bay with 29%.

Table 3.2 Comparison of selected families at Lizard Island, Queensland and North West Cape, Western Australia.

FAMILY	NUMBER OF SPECIES	
	Lizard Is.	North West Cape
Gobiidae	153	31
Labridae	82	47
Pomacentridae	82	37
Apogonidae	44	30
Chaetodontidae	37	23
Serranidae	35	18
Blenniidae	31	25
Holocentridae	23	6
Muraenidae	22	10
Acanthuridae	21	16
Syngnathidae	18	4
Lutjanidae	18	13
Pomacanthidae	16	8
Scorpaenidae	15	8
Scaridae	13	11
Total	801	464

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Table 3.3 Marine fish genera endemic to tropical Australia; *Partial temperate distribution.

GENUS	FAMILY	NO. SPECIES
<i>Brachaelurus</i>	Orectolobidae	1
<i>Heteroscyllium</i>	Orectolobidae	1
<i>Atelomycterus</i>	Scyliorhinidae	1
<i>Aulohalaelurus*</i>	Scyliorhinidae	1
<i>Apistops</i>	Scorpaenidae	1
<i>Cherostorpacae</i>	Scorpaenidae	1
<i>Dampierosa</i>	Scorpaenidae	1
<i>Adventor</i>	Aploactinidae	1
<i>Aploactisoma</i>	Aploactinidae	1
<i>Bathyaploactis</i>	Aploactinidae	1
<i>Karumba</i>	Aploactinidae	1
<i>Neoaploactis*</i>	Aploactinidae	1
<i>Peristrominus</i>	Aploactinidae	1
<i>Hypopterus</i>	Centropomidae	1
<i>Rainfordia</i>	Serranidae	1
<i>Amniataba</i>	Teraponidae	1
<i>Scaevius</i>	Nemipteridae	1
<i>Rhinoprenes</i>	Rhinoprenidae	1
<i>Paradicula</i>	Soleidae	1
<i>Phyllichthys</i>	Soleidae	3
<i>Rendahlia</i>	Soleidae	1
<i>Cantheschenia</i>	Monacanthidae	2
<i>Colurodontis</i>	Monacanthidae	1
<i>Marilyna</i>	Tetraodontidae	1

The Monacanthidae is distributed widely in tropical and temperate seas with approximately 100 species in about 30 to 35 genera. Well over half of the species and nearly all of the genera are represented in Australian seas (Hutchins, 1977). The 20 species and 11 genera that are confined mainly to southern Australia (some extend into the transition zones) by far exceed the numbers found in any other region of similar latitude.

The 13 genera of Antennariidae are summarized by Pietsch (1984). These small, globular fish, well known because of their peculiar feeding mode of attracting prey with a "baited lure", are found throughout warm seas. Eleven of the genera and about half of the 40 species in the family are known from Australia. The southern coastline has given rise to six endemic genera, including five which are monotypic.

Eastern and Western Zones: Extensive zones of intermixing of tropical and temperate faunas occur on the eastern and western coasts. There is a latitudinal gradient or attenuation

Table 3.4 Endemic marine fish families of Australia; *also found in New Guinea.

FAMILY	NO. GENERA	NO. SPECIES	GENERAL DISTRIBUTION
Tetrabranchidae	1	1	Northern*
Brachionichthyidae	1	6	Southeastern
Pataecidae	3	3	Southern
Dinolestidae	1	1	Southern
Caesioscorpidae	1	1	Southwestern
Leptobramidae	1	1	Northern*
Rhinoprenidae	1	1	Northwestern*
Enoplosidae	1	1	Southern
Gnathanacanthidae	1	1	Southern

of the tropical fauna proceeding southward within the transition zones, with progressive replacement of warm water species with cool water forms. Both the eastern and western zones possess endemic faunal elements (Tables 3.6-3.7) which, although not always restricted to the transition areas, have their major occurrence there. These species are frequently among the most abundant representatives of their respective families or genera at a particular locality. The western coast transition zone ranges from about Lancelin (31°01'S) northward to about Point Cloates (22°43'S) and the eastern from Seal Rocks (32°28'S) to the latitude shared by Yeppoon, Queensland and the offshore Capricorn-Bunker Group (23°08'S). Many tropical fishes fail to penetrate these subtropical zones.

The transition or subtropical zones of both coasts are influenced strongly by southerly flowing warm currents which facilitate larval transport from the tropics. Off the western coast, the Leewin Current is responsible for the occurrence of some subtropical species as far south as Albany (35°00'S).

Two areas, lying within the transition zone, that have been studied particularly well in relationship to the fish fauna are the Houtman Abrolhos Islands (Allen, unpubl.) and Lord Howe Island (Allen *et al.*, 1976). Because of their offshore positions in the paths of southerly flowing currents and consequent warmer temperature regimes, they are more directly comparable to mainland areas further to the north. The Houtman Abrolhos Islands (28°35'S) are relatively low-lying limestone shoals and cays. The group is situated about 65 km west of the port of Geraldton, in the path of the Leewin Current. There is rich coral growth and approximately 300 species of inshore fishes. The tropical nature of the fauna is reflected in the high proportion (65%) of tropical Indo-West Pacific fishes. Lesser elements include temperate fishes (25%) and transition zone endemics (6%).

A similar pattern is exhibited at Lord Howe Island, a high volcanic island about 630 km off northern New South Wales and strongly influenced by the East Australia Current. Of 390 inshore species recorded from there about 76% are of

Table 3.5 The most speciose inshore marine fish families occurring in temperate seas of Australia.

FAMILY	SPECIES	GENERA	% OF TEMPERATE SPECIES
Clinidae	36	6	6.0
Syngnathidae	33	22	5.5
Gobiesocidae	23	8	3.7
Gobiidae	22	10	3.7
Labridae	21	11	3.5
Serranidae	20	8	3.3
Monacanthidae	20	11	3.3
Scorpaenidae	18	7	3.0
Urolophidae	14	1	2.3
Rajidae	13	3	2.2
Pomacentridae	12	4	2.0
Tetraodontidae	12	7	2.0
Antennariidae	10	6	1.7
Odaciidae	10	4	1.7
Cheilodactylidae	9	3	1.5
Tripterygiidae	8	6	1.3
Totals	280	117	46.7

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tropical origin, 25% are temperate fishes and about 8% are transition zone forms, including 4% which are endemic in the Lord Howe-Norfolk Islands region.

Provincial Endemism in the Temperate Fish Fauna

Until recently, the taxonomy of the southern fish fauna was insufficiently known to permit a detailed analysis of zoogeographic patterns. Hutchins (in prep.) has made a series of collections and underwater observation stations across the southern half of the continent, compiling a list of approximately 330 inshore fishes. These data provide good insight to the general distribution patterns of the southern fauna (Table 3.8) and, together with taxonomic knowledge of the more speciose groups (Table 3.5), indicate there are two main centres of endemism which correspond to the southwestern and southeastern corners of the continent. Several physical barriers along the southern coast appear to inhibit dispersal in varying degrees. These include: (1) lowered sea temperatures at about Albany in response to the rapid attenuation in this area of the warm Leewin Current; (2) scarcity of shallow reef habitat in the Great Australian Bight between the Recherche Archipelago and Nuyts Archipelago, South Australia (133°20'E); (3) another reef-free "dead zone" of sand-mud substratum at the Murray River outflow between Kangaroo Island (137°00'E) and Robe, South Australia (139°45'E); (4) a similar sandy zone in southeastern Victoria between Wilson's Promontory (46°25'E) and Mallacoota (149°45'E).

Hutchins (in prep.) also notes local differences within the Tasmanian fauna. The north coast has the most species due to a mixing of purely southern fishes with species that are otherwise confined to southern New South Wales and which are sometimes absent from the opposite Victorian mainland. The eastern coast of Tasmania has a slightly diminished fauna compared to the northern coast, but includes several endemic species. The western coast is exposed to strong westerly winds and continual heavy seas; its fish fauna is basically an impoverished version of the eastern coast. An analysis of 131 species recorded by Hutchins indicates that only 2% of the Tasmanian fishes are endemic and most of the fauna consist of species that are distributed widely across southern Australia. More Tasmanian fishes are shared with Western Australia than with New South Wales (82 vs. 68 species).

A noteworthy aspect of the southern fauna is the occurrence in many genera of allopatric eastern and western species pairs (Table 3.9). An increasing number of these pairs have become apparent in recent years as various groups come to the attention of specialists. In a number of cases, a species previously considered to be widespread is shown to consist of distinct eastern and western populations, each warranting specific status.

The reasons for the extensive radiations that have taken place in temperate waters are not entirely clear. Certainly one major factor that has been particularly favourable to the development of east-west species pairs was the alternation of glacial-interglacial epochs during the Pleistocene, with corresponding fluctuations in sea temperatures and shoreline levels. The northward and southward shifts of the boundary between warm temperate and cold temperate water have played a major role in the speciation processes which have occurred in the Australasian shallow-water flora and fauna (Knox, 1980). This boundary, referred to as the Subtropical Convergence, presently lies to the south of Australia, bisecting New Zealand. In the Early Miocene (about 10 mybp), it passed well to the south of New Zealand, gradually shifting northward until it lay across the latitude of Cape Howe, New

Table 3.6 Fish species to the western transition (subtropical) zone. These fishes have their primary breeding populations between Cape Naturaliste and Point Quobba.

FAMILY	SPECIES
Orectolobidae	<i>Orectolobus</i>
Scyliorhinidae	<i>Haelurus labiosus</i>
Urolophidae	<i>Urolophus circularis</i>
Muraenidae	<i>Gymnothorax woodwardi</i>
Gobiesocidae	<i>Alabes brevis, Lepadichthys sandaracatus</i>
Bythitidae	<i>Dipulus caecus</i>
Syngnathidae	<i>Lissocampus satiloguus, Nannocampus subsoesus</i>
Scorpaenidae	<i>Scorpaena sumptuosa, Scorpaena sp., Scorpaenodes steenei</i>
Serranidae	<i>Acanthistius pardalotus, Ellerkeldia rubra, Ellerkeldia wilsoni</i>
Plesiopidae	<i>Trachinops brauni</i>
Glaucosomidae	<i>Glaucosoma hebraicum</i>
Apogonidae	<i>Apogon victoriae</i>
Caesioscorpidae	<i>Caesioscorpis theagenes</i>
Nemipteridae	<i>Pentapodus vitta</i>
Monodactylidae	<i>Schuttea woodwardi</i>
Kyphosidae	<i>Kyphosus cornelii</i>
Chaetodontidae	<i>Chaetodon assarius</i>
Pomacentridae	<i>Chromis westaustralis, Parma occidentalis</i>
Cheilodactylidae	<i>Cheilodactylus gibbosus, Cheilodactylus rubrolabiatus</i>
Labridae	<i>Choerodon rubescens, Coris auricularis, Halichoeres brownfieldi, Suezichthys cyanolaemus, Thalassoma septemfasciata</i>
Opistognathidae	<i>Opistognathus sp.</i>

Table 3.7 Fish species endemic to the eastern transition (subtropical) zone. These fishes have their primary breeding populations between Yeppon, Queensland and Mallacoota, Victoria.

FAMILY	SPECIES
Orectolobidae	<i>Brachaelurus waddi</i>
Urolophidae	<i>Urolophus sufflatus</i>
Batrachoididae	<i>Batrachomoeus dubius</i>
Gobiesocidae	<i>Aspasmogaster costatus</i>
Bythitidae	<i>Dermatopsis macrodon</i>
Scorpaenidae	<i>Centropogon australis, Scorpaena cardinalis</i>
Serrainidae	<i>Acanthistius ocellatus, Ellerkeldia annulata, Ellerkeldia jamesoni, Ellerkeldia maccullochi</i>
Plesiopidae	<i>Paraplesiops bleekeri, Trachinops taeniatus</i>
Apogonidae	<i>Apogon fasciatus</i>
Sparidae	<i>Acanthopagrus australis</i>
Monodactylidae	<i>Schuttea scalarippinnis</i>
Pempheridae	<i>Pempheris affinis</i>
Kyphosidae	<i>Girella elevata</i>
Scorpididae	<i>Scorpius lineolatus</i>
Pomacentridae	<i>Amphiprion latezonatus, Mecaenichthys immaculatus, Parma microlepis, Parma oligolepis, Parma unifasciata, Pomacentrus australis</i>
Aplodactylidae	<i>Crinodus lophodon</i>
Cheilodactylidae	<i>Cheilodactylus vestitus</i>
Labridae	<i>Achoerodus viridis, Pseudolabrus guntheri, Pseudolabrus gymnonotus</i>
Tripterygiidae	<i>Lepidoblennius haplodactylus</i>
Acanthuridae	<i>Prionurus microlepidotus</i>
Monacanthidae	<i>Cantheschenia grandisquamis, Meuschenia trachylepis</i>
Ostraciontidae	<i>Strophurichthys sp.</i>

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Table 3.8 Zoogeographic analysis of the southern Australian fish fauna by state (excluding Tasmania) taken from the survey work of Hutchins; *found throughout southern Australia.

AUSTRALIAN DISTRIBUTION	PERCENTAGE OF TOTAL INSHORE FISHES OBSERVED				
	NSW (150 ssp.)	VIC (124 ssp.)	SA (117 ssp.)	WA (202 ssp.)	Total (328 ssp.)
Widespread*	29.3	33.9	32.5	28.2	20.4
NSW Sub Tropical	14.7	0.8	—	—	20.7
NSW Temperate	28.0	18.5	0.8	—	—
WA Sub Tropical	—	—	—	12.9	17.5
WA Temperate	—	—	2.6	15.8	—
WA, SA & Vic	3.3	18.4	19.7	13.9	10.7
WA & SA	—	0.8	18.8	15.8	9.6
WA, SA & NSW	8.7	1.6	7.6	7.0	4.6
WA & NSW	6.0	2.4	—	5.0	4.0
SA & Vic	1.3	9.7	7.7	—	4.0
Vic	1.3	6.5	2.6	—	2.4
SA, Vic & NSW	4.0	3.2	2.6	—	2.1
SA	—	—	0.8	—	0.3
Uncertain	3.3	4.8	0.8	1.5	3.4

South Wales and Cape Leeuwin, Western Australia in the early Pleistocene. As the colder water moved north in Australia, widespread species may have retreated up the eastern and western coasts, isolating populations and initiating allopatric speciation. The exposure of the Bass Strait land bridge, beginning during the early Pleistocene and resulting in sea level drops of 100 to 210 m (Gill, 1970), provided an excellent opportunity for vicariance in widespread southern species. Present current patterns and the natural barriers discussed above sustain allopatric distributions in many of the resultant species despite the inundation of Bass Strait.

Relationships of the Australian Fish Fauna

The relationship of the Australian fauna with that of New Zealand and other temperate or subtropical areas in the Indo-West Pacific Region is of interest.

New Zealand: The New Zealand fauna consists of about 600 species (Ayling & Cox, 1982), although over half of these are either pelagic or inhabitants of deep, offshore waters. The inshore fauna contains about 200 species, most of which belong to families and genera also found in Australia. The largest families are the Labridae (15 species), Tripterygiidae (15 to 20 species) and Serranidae (eight species), all of which are well represented in Australian seas. About 30% of the inshore species are shared with Australia, including many common species such as the muraenid *Gymnothorax prasinus* and the cheilodactylid *Nemadactylus macropterus*. The remaining 70% of the species are endemic to New Zealand. The close affinity of the Australian and New Zealand faunas may be correlated with their proximity and similar ecological conditions. Nearly all of the shared species are forms which have pelagic eggs and larvae. The trypterygiid fauna of New Zealand, although poorly studied, appears to be entirely endemic. The members of this family are small (mostly less than 100 mm) rocky reef dwellers that attach their eggs to the substratum, exhibit parental care and have a relatively brief pelagic stage.

Southeast Africa: Eastern and southern Africa share a number of similarities with Australia, particularly eastern Australia. Both regions are characterized by well-developed southward flowing warm currents which facilitate the dispersal of tropical fishes from high diversity areas to the north. In addition, both regions have a pronounced temperate fauna, although in most groups this is not as well developed in southern Africa, with the exception of the Sparidae (snappers and breams) and Scyliorhinidae (catsharks) which have experienced explosive radiations.

Knowledge of eastern African fishes is not as precise as that of Australia, but the fauna for the area extending from the Cape of Good Hope northwards, excluding the Red Sea and Gulf of Aden, is estimated to contain about 2,000 species, of which 1,400 are found inshore. Most of the tropical species

Table 3.9 Apparent sister species occurring in southern Australia.

FAMILY	WESTERN SPECIES	EASTERN SPECIES
Gobiesocidae	<i>Aspasmogaster tasmaniensis</i>	<i>Aspasmogaster costatus</i>
Gobiesocidae	<i>Cochleoceps</i> sp. A (undescribed)	<i>Cochleoceps</i> sp. B (undescribed)
Serranidae	<i>Acanthistius serratus</i>	<i>Acanthistius ocellatus</i>
Plesiopidae	<i>Paraplesiops meleagris</i>	<i>Paraplesiops bleekeri</i>
Plesiopidae	<i>Paraplesiops</i> sp. (undescribed)	<i>Paraplesiops poweri</i>
Plesiopidae	<i>Trachinops brauni</i>	<i>Trachinops taeniatus</i>
Teraponidae	<i>Pelates octolineatus</i>	<i>Pelates sexlineatus</i>
Apogonidae	<i>Vicentia</i> sp. (undescribed)	<i>Vicentia conspersa</i>
Mullidae	<i>Upeneichthys vlamminghi</i>	<i>Upeneichthys lineatus</i>
Kyphosidae	<i>Girella tephraeops</i>	<i>Girella elevata</i>
Monodactylidae	<i>Schuttea woodwardi</i>	<i>Schuttea scalaripinnis</i>
Chaetodontidae	<i>Chelmonops truncatus</i>	<i>Chelmonops</i> sp. (undescribed)
Chaetodontidae	<i>Chaetodon assarius</i>	<i>Chaetodon guntheri</i>
Cheilodactylidae	<i>Cheilodactylus gibbosus</i>	<i>Cheilodactylus vestitus</i>
Cheilodactylidae	<i>Cheilodactylus rubrolabiatus</i>	<i>Cheilodactylus spectabilis</i>
Cheilodactylidae	<i>Nemadactylus valenciennesi</i>	<i>Nemadactylus douglasi</i>
Labridae	<i>Achoerodus gouldii</i>	<i>Achoerodus viridis</i>
Tripterygiidae	<i>Lepidoblennius marmoratus</i>	<i>Lepidoblennius haplodactylus</i>

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are part of the widely distributed Indo-West Pacific fauna or at least are derived from it. Many of the former are shared with tropical Australia.

Smith & Smith (1966) state that 25% of South African fishes are endemic, including the Natal fauna which contains many tropical species. The percentage of endemism is much higher if only temperate fishes are considered. Only two families are endemic in inshore South African seas, the monotypic Parascorpididae and the Coracinidae, with two species.

While there are no families shared exclusively by southern Africa and Australia, a single species, the monotypic *Argyrosomus hololepidotus* (a large sciaenid), does exhibit this distribution. The two populations of this species are perhaps relicts of a formerly widespread distribution.

Not notwithstanding the discrepancies between the two temperate faunas, there are some remarkable similarities. The kelp-fishes (Clinidae) have radiated extensively; each area is inhabited by 30 to 40 species. Both regions have a wrasse species of similar large size and general appearance: *Anchichoerops natalensis* in South Africa and two species of *Achoerodus* in Australia. Furthermore, both are inhabited by a large pink snapper (Sparidae) which develops a hump on the forehead with increasing age: *Chrysoblephus gibbiceps* of South Africa and *Chrysophrys auratus* of Australia (and New Zealand).

Japanese Archipelago: The Japanese Archipelago, including the Kuril Islands to the north and the Ryukyu Islands immediately southward, is similar to Australia in that both regions exhibit diverse inshore faunas composed of tropical and temperate elements. Approximately 3,200 species have been recorded from the Archipelago and surrounding waters (Masuda *et al.*, 1984). Of this total, about 2,000 are inshore forms, including 1,600 tropical species and 400 temperate species. Coral reefs are well developed in the Ryukyu Islands and the fish fauna is typically Indo-West Pacific with many species shared with northern Australia. The warm, northerly flowing Kuroshio Current is responsible for the spread of many tropical species along the eastern coast of southern Honshu and to the offshore Izu Islands (34°30'N). The extent of endemism in the Japanese marine fauna is not quantified, but it is certainly far less than that of Australia, probably due to the lack of isolation. Most of the temperate inshore species would be expected to occur in adjacent regions such as Korea, the Russian mainland, Sakhalin, the Kamchatka Peninsula and the Aleutian Islands.

Compared to the gradual and broad transition zone between tropical and temperate seas found in Australia, the boundary between the two is far more abrupt in Japan. Warm temperate or subtropical conditions quickly give way to cold seas, particularly on the eastern coast, due to the southerly flowing Oyashio Current. The fauna consequently is dominated by cold water families that are either unknown or rare in Australian seas. For example, over one-half of the northern inshore fauna is composed of members of the Stichaeidae, Zoarcidae, Hexagrammidae, Cottidae, Agonidae, Cyclopteridae and Liparidae.

One faunal link between Australia and Japan that merits attention involves a number of species and genera belonging to at least 16 families that are shared between the two regions, but which are apparently absent from the intervening tropical zones. Randall (1981) gives numerous examples of anti-tropical or anti-equatorial distributions of Indo-West Pacific fishes. The disjunct distribution of the aploactinid, *Apolactis aspersa*, which is known from China, the Ryukyu Islands, Kyushu and southeastern Australia is typical. Berg (1933) suggests that this sort of distribution originated in the Pleistocene glacial periods when seas were colder, most recently during the late Pleistocene. During this period, the tropical zone was crossed by cool-water forms which were

subsequently isolated as northern and southern populations with the re-warming of tropical seas during interglacial periods. Another popular theory involves their descent into the cooler, deeper waters of the tropics, presumably during the Pleistocene, when lesser depths would have been involved.

MOLLUSCS

There is no accurate estimate of the size of the Australian marine mollusc fauna, although Wilson (1971) suggested that it probably numbers in the tens of thousands. Hedley (1904), Iredale & May (1916), Ashby (1926) and Cotton (1930) published various accounts of biogeographical provinces around the Australian coast based on mollusc species distributions.

These authors all recognized that the coastal fauna of tropical northwestern Australia has many different species to that of the coast of eastern Queensland and that there also are differences between the faunas of southwestern and southeastern Australia. The provincial names which they introduced have been used widely, although there has been little agreement about the location of the boundaries.

Most families of living marine molluscs are represented in the Australian fauna. Inadequate taxonomic knowledge of most families makes detailed analysis of generic distributions difficult. At the species level, however, distribution patterns are fairly clear. Some families (*e.g.* Strombidae) are strictly tropical and represented only in the north of Australia. Many (*e.g.* Cardiidae, Mytilidae, Cypraeidae) which are represented strongly in the north have a few southern temperate species. A few families (*e.g.* Haliotidae) are represented most strongly in the south. Some families are characterized by widely distributed species while in others species tend to be geographically restricted. There are three families which are now confined to Australia although they had a much wider distribution in earlier times.

Endemic Families

Trigoniidae: This bivalve family had a cosmopolitan distribution throughout the Mesozoic, but disappeared at the close of that era, except for one genus, *Eotrigonia*, which survived in the early Tertiary of southern Australia (Darragh, 1986). Today, a single genus, *Neotrigonia*, survives in Australian waters. It has six living species, one in the tropical north, one in the southwest and four in the southeast. Although opinions vary on the origins and affinities of *Neotrigonia*, Darragh (1986) believes that it evolved abruptly in the Middle Miocene from its southeastern Australian Paleogene ancestor, *Eotrigonia*.

Campanilidae: *Campanile symbolicum* is the sole surviving species of the cerithiacean family Campanilidae which had a long lineage, with several genera and many species in the Tethys Sea during the Tertiary (Houbrick, 1981). Fossil Australian species are known from the Pliocene of South Australia, *i.e.* within the Austral Indo-Pacific Province. The single living species is found in abundance in the southwest of Western Australia from Geraldton to Esperance. It also is represented much further east, in the rich early Pleistocene fossil deposits of the Roe Plain (Ludbrook, 1971). It is a Tethyan relict.

Diastomatidae: *Diastoma melanoides* is the sole surviving species of this cerithiacean family. The group is best known from the Eocene of the Paris Basin, but was once widespread throughout Tethys (Ludbrook, 1971; Houbrick, 1981). The genus is represented in the Pliocene of South Australia, *i.e.*

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within the Austral Indo-Pacific Province. *Diastoma melanoides* is rare and lives at a few localities in western South Australia and on the southern coast of Western Australia. It may be regarded as a Tethyan relict.

Selected Families with Widespread Distribution

Haliotidae: The haliotids or abalone are vegetarian archaeogastropods inhabiting hard substrates. Reproduction involves the synchronous spawning of large quantities of eggs and sperm. Planktonic larval development is short (usually a few days) and lecithotrophic. The family is distributed widely in modern shallow tropical and temperate seas, but consists of only about 50 living species, almost half of which occur in Australia. Centres of relatively high diversity are in the temperate waters of the western coast of North America (eight species) and southern Australia (13).

All the tropical species and the majority of the temperate ones live more or less solitarily, but some of the latter (for example *Haliotis cyclobates*, *H. roei*, *H. ruber*, *H. laevigata*, *H. conicopora*) are gregarious. Their populations are a conspicuous feature of the southern shallow water fauna and form the basis of an important abalone fishery.

Of the four common haliotids in tropical northern Australia, three are coral reef species which occur both in the northeast and the northwest and have wide Indo-West Pacific distributions. The fourth species (*Haliotis squamata*) inhabits turbid coastal waters and is endemic in the northwest, but ranges south to Shark Bay in the western transition zone. Three additional rare species of uncertain taxonomic status have been described as eastern Queensland endemics.

All of the temperate Australian haliotids are endemic. Two species (*Haliotis emmae*, *H. cyclobates*) are confined to the southern coast between South Australia and Bass Strait. Two (*H. ruber*, *H. coccoradiata*) range from the eastern transition zone into South Australia and Victoria, respectively. Five (*H. semiplicata*, *H. scalaris*, *H. roei*, *H. laevigata*, *H. conicopora*) range from the southern part of the Western Transition Zone eastwards to South Australia or Victoria. The southern coast fauna is a mixture of southeastern and southwestern species.

Haliotis roei—*H. ruber* and *H. scalaris*—*H. emmae* appear to be western-eastern species pairs which just fail to establish sympatry in South Australia. This is an oft-repeated pattern among southern Australian molluscs.

Curiously, there are no Tertiary fossil haliotids known from southeastern Australia. This may be because their hard substrate habitat is rarely represented in the fossil record. Despite this anomaly, the high concentration of species in southern Australia is likely a result of a long family history in the region and the prominence there of algal-covered rocky substrates.

Although the generic taxonomy is unreliable, several genera (or subgenera) are represented in the Australian fauna and the southern ones (*Schismotis*, *Exohaliotis*, *Notohaliotis*, *Marinauris*, *Neohaliotis*) are endemic to that region. Whether these taxa were derived from ancient Tethyan stock and evolved within the Southern Australian Region after its isolation or whether they are Palaeoaustral relicts cannot be decided on the present evidence.

Trochidae: This archaeogastropod family is one of the largest in the Class Gastropoda. Like the haliotids, trochids spawn large numbers of small eggs and have short-lived, lecithotrophic, planktonic larvae. Although the family is well represented in all shallow and most moderately deep waters

of the world, it is unusually speciose in the temperate and subtropical zone of southern Australia. The taxonomy of the family is known poorly at both the specific and generic level.

There are at least 50 trochid genera or subgenera and probably several hundred species in the Australian fauna. Approximately two-thirds of these are southern or transition zone endemics. Some of the southern taxa may have had their origins in the Palaeoaustral and southeastern Australian faunas of the Tertiary, but many are undoubtedly derivatives of Tethyan ancestors. Tethyan affinities are evident in such southern groups as *Austrocochlea*, *Astele* and *Thalotia*. Regardless of the origins of the taxa, the extraordinary proliferation and radiation of the Trochidae in the temperate waters of southern Australia is one of the features of the region.

Most of the tropical species in northern Australia, such as the several species of *Trochus*, are distributed widely in the Indo-West Pacific. *Trochus (Tectus) pyramus* and *Chrysostoma zeus*, however, are obviously recent derivatives from modern Indo-West Pacific species complexes and are endemic to the mid-western coast of Western Australia. The pinching off of new species on the subtropical western coast, peripheral to the main distribution of Indo-West Pacific genera and subgenera, is a common feature among Western Australian molluscs. Probably this feature had its origins during the periodical latitudinal shifts of climatic zones about the fulcrum of North West Cape during the Pleistocene.

Strombidae: Females in this mesogastropod family spawn numerous eggs in a gelatinous egg-mass from which hatch free-swimming, planktotrophic veliger larvae providing the species with a capacity for wide dispersal.

The family is tropical and subtropical. It originated in Tethys during the middle Tertiary and flourished until the early Pleistocene, with a subsequent decline in diversity. The five living genera, *Strombus*, *Lambis*, *Terebellum*, *Tibia* and *Rimella*, are represented today in the Indo-West Pacific Region, but only *Strombus* now occurs in the tropical Eastern Pacific and Atlantic regions. All but *Tibia* are found in northern Australia.

Within the Indo-West Pacific Region there are about 56 living species which exhibit distribution patterns typical of species with planktotrophic larvae. Many of these widely distributed species are polytypic (Fig. 3.10) and peripheral endemism is common. The fossil record shows that the break-up of widely distributed species into separated geographical races and the isolation of relict species now endemic in peripheral areas has been a result of contraction of range since the early Pleistocene (Abbott, 1960).

In northern Australia, 21 species of *Strombus*, five *Lambis*, one *Rimella* and one *Terebellum* have been recorded, half the total number of species known from the Indo-West Pacific Region. None are endemic to Australia, although there are four endemic subspecies: *S. vittatus campbelli* occurs across the whole northern coast, *S. aurisiana aratum* occurs on the mainland eastern coast of Queensland and *S. urceus orrae* and *S. vomer iredalei* occur on the northern coast of Western Australia and the Northern Territory.

Of the 28 species found in northern Australia, 13 are common to both the eastern and western coasts, 10 are found only on the eastern coast of Queensland and five are exclusive to the western coast.

Abbott (1960) observed that there are two suites of stromb species requiring different habitat conditions within the Indo-West Pacific Region. One group, typified by *Strombus canarium*, *S. urceus* and *S. vittatus*, inhabits the nutrient-rich shores of continents or well-vegetated volcanic islands and tends to have restricted geographical distributions, often

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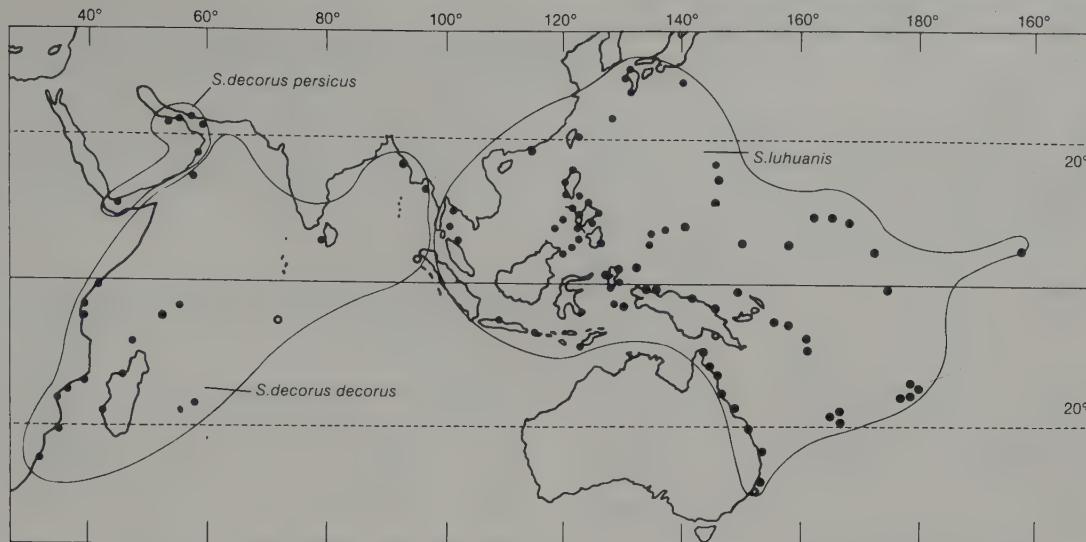


Figure 3.10 Geographical distribution of two species of *Strombus* in the Indo-West Pacific. (After Abbott, 1960)

confined to the central part of the Region. The other group, typified by *Lambis* spp., *S. mutabilis*, *S. erythrinus*, *S. luhuanus* and *S. lentiginosus*, is limited to clear, oceanic waters of coral islands and reefs. Species of the second group tend to be distributed more widely.

In eastern Queensland, both habitat types are extensive, but in the Northern Territory and Western Australia north of North West Cape, clear water coral reef habitats occur only on a few outer reefs, such as those of the Monte Bello and Barrow Islands and the shelf-edge atolls. Some of the faunistic differences between northwestern and northeastern Australia may be explained in terms of the differential frequency of available habitat. For example, *Strombus erythrinus*, *S. luhuanus*, *Lambis scorpius* and *L. crocata* are common on the Great Barrier Reef, but apparently absent in the west (Fig. 3.10). *Strombus lentiginosus*, *L. lambis* and *L. chiagra*, also common on the Great Barrier Reef, are known from only a few coral reef localities in Western Australia. On the other hand, the absence of species such as *S. canarium* from the western coast and, conversely, species such as *S. urceus* from the eastern coast, is difficult to explain in ecological terms and historical interpretations seem to be required.

In many mollusc families there are a few widespread Indo-West Pacific species which range far south of the tropics on both sides of Australia. *Strombus mutabilis* is a striking example (Fig. 3.11), extending as far north as southern Honshu in Japan, as far south as Durban in eastern Africa and as far east as the Tuomotu Archipelago in the Pacific. In Australia, it is common as far south as Cape Naturaliste on the western coast and central New South Wales on the eastern coast. Such species must be eurythermal and have great capacity for larval dispersal.

Cypraeidae: This family is a typical example of a group which has its centre of greatest species-richness in the central part of the Indo-West Pacific (Foin, 1976). Cypraeids show all the species distribution patterns described for the Strombidae but, in addition, include some temperate species in the waters of southern Australia.

The majority of Australian species (≈ 60) is found in the north; most are distributed widely in the tropical Indo-West Pacific Region. There are only three endemic species in tropical Australia, *Cypraea brevidentata* and *C. decipiens* in northern Western Australia and *C. xanthodon* in eastern Queensland. Many of the Indo-West Pacific cowries are polytypic, but excessive taxonomic splitting makes zoogeographic analysis of allopatric subspecies impractical. With few exceptions, the tropical species range across northern Australia from west to east. There are a few cases, like *C. mappa* in the east and *C. histrio* in the west, which have been recorded from one side of the continent only, but these distributions may be artefacts of inadequate collecting. One group of species, however, *C. langfordi*, *C. hungerfordi* and *C. hirasei*, appears to be confined to the deeper water zone off the coast of southern Queensland. Interestingly, these cowries are all found in similar habitats and latitudes of subtropical Japan and Taiwan.

In Western Australia, 52 species are recorded, of which four extend no further south than the Kimberley coast, a further 15 fail to pass Ningaloo Reef on the western side of North West Cape, while the majority, 33 species, end their southern range at some point in the transition zone on the central western coast. At least two species, *Cypraea caputserpentis* and *C. helvolva*, both of which are distributed widely in the Indo-West Pacific Region, pass around Cape Leeuwin and may be found regularly as far east as Albany. A similar latitudinal attenuation of tropical species occurs down the eastern coast between Sandy Cape in southern Queensland and central New South Wales. The species which extend far south of the tropical zone on the western coast are generally the same as those which do this on the eastern coast.

Perhaps the most striking feature of cowry distribution patterns in Australia is the presence of several endemic groups in the temperate Southern Australian Region. One of these is a group of five species known by the generic name *Notocypraea*. The fossil genus *Notoluponia*, from the Oligocene-Miocene of southeastern Australia, appears to be the group's ancestor. The only living relatives are the temperate South African species of *Cypraeovula*. Clearly, from the

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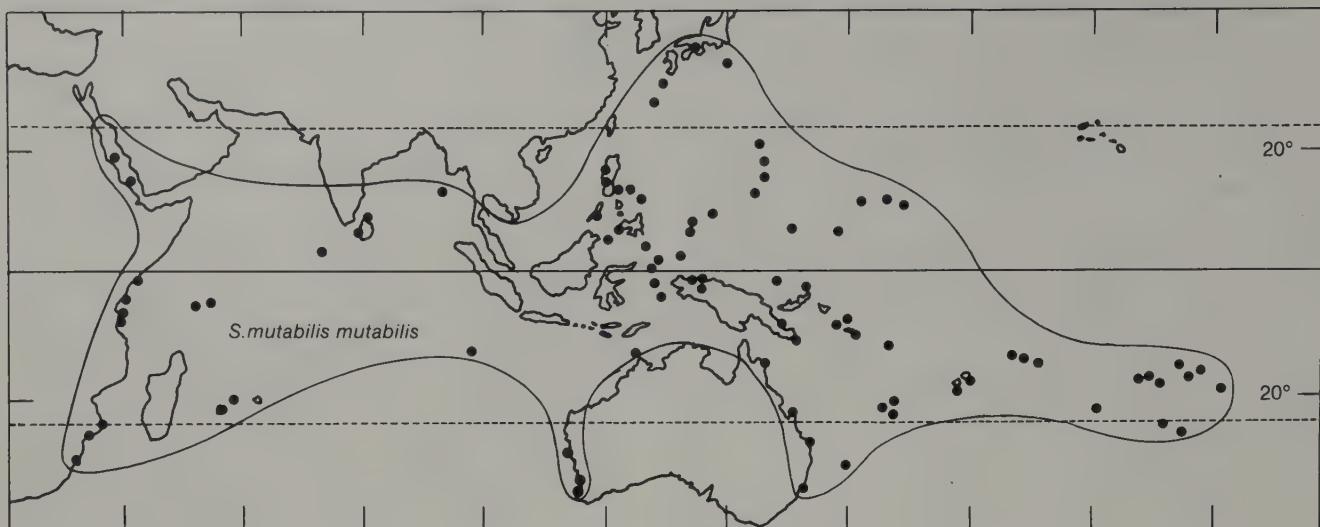


Figure 3.11 Geographical distribution of *Strombus mutabilis* in the Indo-West Pacific. (After Abbott, 1960)

fossil record, *Notocypraea* is an ancient, endemic southern Australian group quite distinct from the living tropical Indo-West Pacific cowries.

Umbilia, another endemic southeastern Australian genus with a long Tertiary lineage within the region, has two living species (*U. hesitata* and *U. armeniaca*) but no other extant relatives. Some authors place *Umbilia* and *Notocypraea* with the South African *Cypraeovula* in the Tribe Cypraeovulini. Whether or not this is correct, *Notocypraea* and *Umbilia* may be regarded as living relicts of the ancient southeast Australian early Tertiary cypraeid fauna, possibly with their origin in the Palaeoaustral Region.

A third endemic southern Australian genus is *Astrocypraea*, which had several middle Tertiary species, but only one living survivor (*A. reevei*). This group also may have its origins in the ancient southeastern Australian Tertiary fauna or it may be derived from Tethyan elements. The latter is certainly the case for the fourth endemic group, *Zoila*. This endemic Australian group has five living species, four of which live on the South West Shelf and one on the North West Shelf between North West Cape and Broome. Unlike *Notocypraea* and *Umbilia*, *Zoila* has obvious links with Tethyan groups, *Bernaya* and others, sometimes linked in the Tribe Bernayini. Today, there are three species of this tribe living in the Indo-West Pacific and Caribbean Regions which are considered to be relicts of the Tertiary Tethyan fauna and appear to be distant relatives of the Australian species of *Zoila*.

In summary, the Cypraeidae illustrates several significant features of the Australian molluscan fauna. The majority of species live in the tropical shallows of northern Australia and are widespread in the Indo-West Pacific Region; they are modern derivatives of the fauna which has evolved within that region since the late Tertiary. In the temperate south there are two groups, *Notocypraea* and *Umbilia*, which are relicts of the ancient fauna endemic to southeastern Australia and which have evolved there quite independently from the species of the Indo-West Pacific Region since the early Tertiary. In the warm temperate south and west, *Zoila* and, perhaps, *Astrocypraea* are derivatives of Tethyan taxa which invaded and radiated within the region since the middle Tertiary.

With the apparent exception of the relict species of the Bernayini, tropical cowries have planktotrophic veliger larval stages. All four of the southern Australian endemic groups have direct development, totally lacking a larval dispersal stage (Wilson, 1985). This may be interpreted as an adaptation to cooling conditions and increasing seasonality in the Southern Australian Region since the middle Tertiary. If, however, *Umbilia*, *Notocypraea* and the South African *Cypraeovula* are ancient Palaeoaustral groups, they may have had a cold-water origin.

Conspicuous intra-population and clinal variability, which is a feature of the southern cowries, is probably a consequence of their direct development.

Volutidae: Voluts are predatory neogastropods which lay egg-masses from which hatch crawling juveniles. Perhaps as a consequence of the absence of a pelagic larval stage, the species tend not to be widespread and the majority of Australian genera are endemic.

Weaver & du Pont (1971) recognize six subfamilies, all of which are represented in the Australian fauna. Following their classification (with some modifications) there are 16 genera in Australia, of which 11 are endemic.

Melo, *Aulica* and *Aulicina* range from the Indo-Malayan area of the central Indo-West Pacific into both northwestern and northeastern Australia. *Melo* has one species endemic to the southwestern corner and the southern coast as far east as South Australia.

Amoria is a relatively large genus ranging across the whole of northern Australia. In the west, two species (*A. damoni*, *A. grayi*) range southwards into the Western Transition Zone, while one (*A. diamantina*) is endemic there.

Volutoconus and *Nannamoria* occur in both the northwest and northeast. *Cymbiolacca* is a large genus peculiar to eastern Queensland, though one species extends into New South Wales. There is little or no fossil record for any of these northern groups, but they appear to be modern derivatives of the Indo-West Pacific fauna. *Cymbiolacca* may be an exception.

The groups *Athleta* (*Ternivoluta*), *Zebramoria*, *Relegamoria*, *Cymbiolista* and *Cymbiolena* are characteristic of the New South Wales coast, although there is a little overlap into southern Queensland. *Notovoluta* has its main strength in

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southern and southwestern Australia, but one species occurs in southern Queensland. *Ericusa*, *Amorena* and *Livonia* are southeastern genera which range from southern Queensland to western Victoria or South Australia. *Notopeplum*, *Paramoria* and *Cottonia* are characteristic of the southwest. Some of these groups have a long fossil lineage in the southeastern Australian Tertiary and they may represent an autochthonous element surviving since the days of the Palaeoaustral Region.

Teramachia and *Lyria* are cosmopolitan genera represented in the Australian fauna. Species of *Teramachia* inhabit deep water (outer shelf and slope zones) in the Caribbean, Japan and the Philippines. The two Australian species were described recently from the North West Shelf of Western Australia. *Lyria* has several species in eastern and southern Australia, including the monotypic subgenus *Lyreneta*, endemic to the coastal waters of New South Wales. *Athleta* was once a cosmopolitan genus, but is now reduced to two relict groups, one in South Africa and the other, the subgenus *Ternivoluta*, represented by two species in eastern Australia.

From these data, at both generic and species levels, the volutid fauna of the temperate and subtropical southern half of Australia clearly is very different to that of the tropical north, although there is overlap in the Eastern and Western Transition Zones.

At the species level, there are conspicuous differences between the northeast and northwest. In the genus *Amoria*, for example, there is a suite of eight species characteristic of the northwest, two of which extend across the north to the northern end of the Great Barrier Reef (*A. turneri*, *A. damoni*) and two which extend south of North West Cape into the Western Transition Zone (*A. grayi*, *A. damoni*). In the northeast, a suite of five species is confined to the Great Barrier Reef area.

Similarly, there are also conspicuous differences between the southeast and southwest. There are six species endemic to the Western Transition Zone and 10 to the Eastern Transition Zone. On the southern coast between Cape Leeuwin and Bass Strait there are 13 species: seven are restricted there, two range onto both the eastern and western coasts, two are shared with the eastern coast and two are shared with the western coast. There are no species confined to the Bass Strait-Tasmania area.

The distribution patterns in this family are quite different to those of groups which have planktotrophic larvae and planktonic dispersal capacity. Unlike other groups, the tropical Australian species are not widespread in the Indo-West Pacific and tend to be restricted in range even within the northern Australian region. Not surprisingly, this family exhibits the highest degree of species endemism in the northwest and northeast. Similarly, there are species peculiar to the southwestern and southeastern coasts. Further study is needed to determine which southern volutid genera have their origins in the palaeoastral fauna and which derive from Tethyan ancestors.

Mytilidae: Female mytilids spawn vast quantities of eggs and the veliger larvae are planktotrophic. Some adults are byssal-attached fouling organisms and have the potential for long-range dispersal by shipping or rafting. The family is cosmopolitan and all the shallow water subfamilies are represented on the Australian coasts.

There are about 19 genera in Australia, of which the monotypic *Austromytilus* of southeastern Australia is the only endemic genus. Seven genera are represented in both tropical and temperate waters of Australia and elsewhere. Nine, which are found only in the tropical north of Australia, are wide ranging in the Indo-West Pacific and beyond.

In addition to *Austromytilus*, there are three genera in southern and eastern Australia which may be regarded as temperate. These are of particular biogeographic interest for differing reasons. *Mytilus* is represented by a form of *M. edulis*, a circumpolar and bipolar species found in similar latitudes in the North Atlantic and North Pacific, South America, South Africa, New Zealand and certain sub-Antarctic islands, as well as in southern Australia. It occurs as a Pliocene fossil in Australia and New Zealand and its bipolar distribution cannot be explained by rafting in modern times.

Trichomya has a Pliocene record in southeastern Australia, New Zealand and Japan. *Trichomya hirsutus* is a surviving species living in southeastern Australia. This also is a temperate group which appears to have jumped the Pacific equator at some time. The genus *Xenostrobus* has three species living in southern Australia and one (*X. australis*) in temperate waters of Japan which appears to be closely related to the Australian and New Zealand *X. pulex*. These connections of the southern Australian temperate mytilids with the Northern Hemisphere have parallels in other phyla.

There are approximately 51 species of mytilid in Australia. Some 35 of these are widespread in the Indo-West Pacific Region, most recorded in both the northeast and northwest of Australia. In Western Australia, all but some coral-boring species of *Leiosolenus* extend well down the western coast. *Septifer bilocularis*, *Modiolus auriculatus*, *Botula fusca* and *Lithophaga gracilis* are examples of very widespread Indo-West Pacific species which range as far down the coast as Cape Leeuwin or beyond.

Septifer bilocularis is an ecologically ubiquitous species which seems to be found in shallow water throughout the Indo-West Pacific, in both oceanic and coastal conditions.

Modiolus auriculatus is representative of a suite of tropical mollusc species which require clear oceanic water and are distributed widely on coral reefs throughout the Indo-West Pacific. On the turbid northwestern coast between North West Cape and Darwin, it is replaced by an undescribed endemic congener, although it is common on the oceanic atolls of the North West Shelf edge. *Modiolus philippinarum*, *M. micropterus* and *M. proclavis*, on the other hand, are representative of a suite of species inhabiting nutrient-enriched continental shores. Members of this group tend to have more restricted geographic distributions, often confined to the central Indo-West Pacific Region including northern Australia.

There is only one endemic "tropical" mytilid, *Brachidontes ustulatus*, which ranges southwards from the Kimberley region of coastal Western Australia then eastwards to South Australia. Discounting that unusual species, there are about 16 southern species, most of which are endemic and common to the southeast and southwest. *Trichomya hirsutus* and *Austromytilus rostratus* are exceptions; both are confined to the southeast and range from New South Wales into Bass Strait and eastern South Australia. Several southern Australian species (*Mytilus edulis*, *Xenostrobus pulex*, *X. securis*, *Modiolus areolatus*) also are found in New Zealand. *Musculista senhousia* is a recent introduction from Japan. This mussel also was introduced to California earlier this century, presumably from shipping, as a fouling organism.

Cardiidae: There are 10 cardiid genera represented in the Australian fauna (Wilson & Stevenson, 1977), none of which are endemic. Only three are confined to the Indo-West Pacific and Southern Australian Regions (*Vetricardium*, *Fragum*, *Fulvia*). *Nemocardium (Pratulum)* is endemic to southern Australia and New Zealand today, but is represented by several Tertiary fossil species in Europe.

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Of the 34 Australian species, 25 are widespread in the Indo-West Pacific Region and occur in both northwestern and northeastern Australia. An additional three species (*Acrosterigma dupuchense*, *A. fultoni*, *A. roseomariensis*) are endemic to the waters of the northern coast of Western Australia. *Acrosterigma vlamingi* and *A. marielae* are endemic to central west coastal waters. *Fragum erugatum* has an unusual distribution, extending from the Dampier Archipelago on the northwestern coast to Geographe Bay in the southwest. All of these Western Australian endemics have their closest affinities with the Indo-West Pacific fauna. No indigenous cardiids have been described from the eastern coast of Australia.

There are three endemic species which range across the southern coast of the continent, all of which extend well up the eastern and western coasts (*Acrosterigma cygnorum*, *Nemocardium (Pratulum) thetidis*, *Fulvia tenuicostatum*). Each of these species has fossil antecedents in the southeastern Australian Tertiary.

Two Western Australian species (*Acrosterigma reeveavum*, *Fragum erugatum*) have made brief incursions around Cape Leeuwin and as far east as South Australia, where they are represented by Quaternary fossils.

Summary

The Northern Australian Mollusc Fauna: With some notable exceptions, mollusc families are much more speciose in the north of Australia than in the south. There is very little generic endemicity and only a relatively small amount of species endemicity ($\approx 10\%$) in the north. The majority of species are distributed widely in the Indo-West Pacific Region. Exceptions are most common in families which lack pelagic larvae (such as the Volutidae) and are characterized by restricted species distribution. Families which have long-lived planktotrophic larvae, and hence a capacity for wide dispersal (Strombidae, Mytilidae), exhibit no species endemicity in northern Australia although there may be some subspeciation within the region. In both eastern and western Australia there is a latitudinal attrition of tropical species beyond about 25°S.

Considering the northwestern and northeastern coasts separately, there are significant faunistic differences in some groups (for example the Volutidae), but close affinities are obvious. Some of the differences between the two sides of the continent are due to the differential extension of widely distributed Indo-West Pacific species down both sides of tropical Australia. Such differences can be accounted for, in part, by ecological factors such as the greater development of coral reef habitats in the east.

In many tropical groups, molluscs of coral reefs tend to be distributed more widely in the Indo-West Pacific Region and more often polytypic than species which inhabit rocky or soft substrates of turbid coastal waters. The latter species often are of restricted distribution in the central part of the Region.

The Southern Australian Mollusc Fauna: There is significant generic endemicity among southern Australian molluscs and a very high level of species endemicity (probably over 95%). Many endemic genera (such as *Notocypraea*, *Ternivoluta*) have fossil lineages in the southeast of the region dating back to the early Tertiary, indicating that they may be survivors from the ancient Palaeoaustral fauna. Other southern Australian endemic genera are relicts of once widespread Tethyan groups which have become extinct elsewhere during or since the Tertiary (for example *Zoila*, *Campanile*, *Miltha*,

Diastoma). The Palaeoaustral elements seem to be most conspicuous in the southeast and the Tethyan elements in the southwest.

Most non-endemic genera are common to the Southern Australian Region and the Indo-West Pacific Region, indicating that the faunas of both regions are derivatives, in part, of the Tethyan fauna. The remainder are cosmopolitan genera such as *Acrosterigma*, *Modiolus* and *Mytilus*.

Large numbers of species range across the entire southern coast of Australia. Many extend up both the eastern and western coasts, although Cape Howe in the east and Cape Leeuwin in the west are termini for a number of species. Northwards of these points there is an attenuation of species (Wilson & Stevenson, 1977; Wells, 1980), the reverse of the situation described for the northern fauna.

There are, however, significant differences between the southeastern and southwestern faunas. In the western transition zone north of Cape Leeuwin, there are many endemic species, some of which range across the southern coast to South Australia or Bass Strait. Conversely, in the eastern transition there are many endemics, some of which range through Bass Strait to western Victoria or the Great Australian Bight.

A few southern Australian species are shared with New Zealand. These invariably are species which have long-lived planktotrophic larvae and some may be recent immigrants to New Zealand from Australia. Ancient historical connections, however, are evident and some modern similarities can be traced back through fossil lineages to common Palaeoaustral ancestors.

CORALS

For many, scleractinian corals are the epitome of tropical marine organisms and their distribution patterns are worthy of study in their own right. Further, corals create a reef habitat which supports countless other organisms, linking the distribution patterns of corals with those of other groups.

The distribution of coral reefs has been a subject of intense scientific study since the days of Charles Darwin. For most of this time, minimum water temperature has been assumed to set the latitudinal limits of coral reef development. It is true that "no significant reefs occur where temperatures during the year fall below about 18° except for very short periods" (Wells, 1957). Whether or not lower temperature is the sole causal factor is questionable. Even where bathymetric conditions are suitable, factors such as increased seasonality and competition with other organisms may begin to operate at the edge of the tropical zone and combine with lower temperature to inhibit coral growth.

A striking feature of coral distributions within the Indo-West Pacific Region is the homogeneity of the fauna. Most genera and many species are ubiquitous from East Africa to French Polynesia and, unlike other groups of marine organisms, there is very little peripheral endemicity (Potts, 1983; 1985). There is however, a central high generic and species diversity focus in the area between Southeast Asia and northern Australia (Stehli & Wells, 1971). This zone has by far the richest coral fauna of the world, with more than 70 genera (J.E.N. Veron, pers. comm.); compared with 25 genera in the Western Atlantic. Its continental shelves are richly endowed with coral reefs, containing about 53% of the Indo-West Pacific reefs (Potts, 1983). Coral faunas become increasingly impoverished with increasing distance from this centre (Veron, 1985). Rosen (1975) associated the latitudinal diversity gradient with decreasing sea temperature and the easterly gradient across the western Pacific with distance and larval dispersal capacity.

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Despite the very wide geographical range of many coral species, genetically distinct subspecies appear to be the exception. High intra-specific variation, however, is common and is interpreted by Potts (1983) to imply evolutionary disequilibrium. He suggested that Indo-West Pacific corals were subjected to chronic evolutionary disturbance by the high frequency of large scale sea-level fluctuations throughout the Pleistocene (Chappell, 1981). Substantial sea-level falls repeatedly laid bare much of the shelf areas of Southeast Asia and northern Australia and reduced the habitable zone (for corals) around most Pacific islands to a narrow wave-bashed rim. The average time that any given bathymetric level has remained within the zone of coral reef growth (*i.e.* 0–20 m) was only 3,200 years. Potts (1983; 1984; 1985) argued that, with a generation time commonly exceeding 10 years, coral populations would pass through only 350 generations in such a span. In fact, many corals appear to have no physiological senescence. Size and reproductive output of individual colonies tend to increase with age because of vegetative growth. Some coral colonies may live for several centuries. These large, ancient clones are likely to make disproportionately large genetic contributions and there is likely to be generation overlap. Consequently, within a given time, corals have a much lower probability of achieving significant genetic divergence than other marine organisms with shorter generation periods.

Frequent drastic disruption by Quaternary sea-level changes has invoked chronic evolutionary disturbances within local populations, enhancing the accumulation of intra-population variability, but preventing speciation from approaching completion.

According to Potts (1983; 1984; 1985), such a model explains the relatively high diversity of the central Indo-West Pacific, the attenuation away from this centre and the relative homogeneity of the Indo-West Pacific coral fauna. In his view, the central zone has been a reservoir of coral species since the late Tertiary and there has been little speciation since the beginning of the Pleistocene sea-level fluctuations. The latter caused repeated local extinctions on oceanic reefs of the central Pacific. Recolonization was from larger refugia in the Western Pacific and the shelf areas of the central zone by species capable of long distance dispersal. These were the species most tolerant of environmental extremes and least likely to differentiate. The easterly diversity gradient is interpreted, thus, in terms of extinction rates, dispersal capacity and distance.

McManus (1985) argued that Quaternary sea-level fluctuations enhanced speciation within the central Indo-West Pacific Region which became the centre of origin of the region's coral fauna.

Rosen (1984) also argued that eustatic changes enhanced speciation, but he believed that the high diversity of the central zone is due to accumulation of immigrant new species originating among the western Pacific islands.

There is much to learn about the effects of sea-level fluctuations on marine animal evolution and distribution patterns in the Indo-West Pacific. A central zone high diversity focus and outward diversity gradients seem to be common to all groups of animals. Geographical homogeneity and high levels of intra-specific variability, which are peculiar features of coral distribution patterns, seem likely to be the result of the unusual life history of these organisms and their genetic responses to repeated disturbance during the Pleistocene.

The northern Australian coast is part of the central Indo-West Pacific focus of coral high diversity. Data published by Wells (1955) showed a steady attenuation of coral genera from north to south down the length of the Great Barrier Reef. More recent data have shown that there is little change in the composition of the coral fauna throughout the length

of the Reef (Veron, 1985) and a rather abrupt cut off in diversity occurs at the southern end. Species-impoorered coral reefs occur, however, as far south as the Solitary Islands in northern New South Wales (Veron, 1974) and at Lord Howe Island (Veron & Done, 1979); some species extend their range as far south as Sydney.

A latitudinal diversity gradient occurs down the coast of Western Australia, but it, too, is less marked than previously thought. Major coral reef systems are developed as far south as the Houtman Abrolhos Islands, off the coast of Geraldton in latitude 29°S. Veron (1985) recorded 44 hermatypic genera and more than 157 species at the Abrolhos and currently lists 183 from that locality (pers. comm.). Some tropical species extend their range to Geographe Bay and onto the southern coast as far east as Cape Arid.

Not a great deal is known about the larval life of corals. Most planulae survive for only a few days (Connell, 1973), but some may survive much longer. In eastern Australia, the East Australia Current flows strongly down the length of the Great Barrier Reef and, given the semi-continuous reef habitat providing stepping stones for species with planktonic larvae, the lack of a latitudinal diversity gradient there is not surprising. But, beyond latitude 25°S, many species reach their lower limit of temperature-correlated tolerance, beyond which coral growth is inhibited. The existence of coral reefs at the Solitary Islands and Lord Howe Island, though depauperate, may be attributed to transport of temperature-tolerant, vagile species southwards by the East Australia Current and its gyres.

In Western Australia, the warm Leeuwin Current along the shelf-edge is responsible for establishment of the Abrolhos coral reefs which lie in its path. Only a handful of coral species, and no reefs, occur on the adjacent mainland. The Leeuwin Current apparently carries the larvae of some tolerant corals even further south where they thrive as individual colonies, but form no reefs. There is evidence that during Pleistocene interglacials the Leeuwin Current was even more effective than it is today; fossil coral reefs, including *Acropora* species, occur at Rottnest Island (Szabo, 1979).

The question arises whether temperature tolerance and dispersal capacity are the primary factors which determine the southern limits of coral species and coral reefs. From studies of Abrolhos coral reef systems, Johannes *et al.* (1983) suggested that the latitudinal limits of coral reef development are often set by competition of macroalgae with corals and that macroalgae are favoured at high latitudes by high nutrient concentrations, moderate water temperatures (for macroalgae) and possibly by reduced grazing pressure. In the absence of up-welling or land-based sources of nutrient-enrichment, low latitude coral reefs are characterized by low biomasses of fleshy algae. Schools of herbivorous fishes, such as siganids and acanthurids, exert heavy grazing pressure on macroalgae growing on tropical coral reefs. At higher latitude reefs such as the Abrolhos, the variety and number of herbivorous fishes are less (Allen *in* Wilson & Marsh, 1979), possibly giving a competitive advantage to the macroalgae.

Within the Great Barrier Reef region, there are differences in community structure and, to a lesser extent, species composition between coral communities of the inner and outer zones (Done, 1982). These differences apparently relate to environmental differences such as tidal range, salinity, siltation, nutrient enrichment and wave energy, but there are no unequivocal data on the mechanisms by which the differences are maintained.

Noting that most corals have short-lived planktonic planulae, that most coral communities tend to repopulate themselves and that ocean currents in the area are long-shore (*i.e.* north to south), Done (1982) argued in favour of limits to dispersal as the primary mechanism, rather than differential survival of

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recruits. In our context, however, the longitudinal faunal zonation of the Barrier Reef is a regionally internal ecological phenomenon. Although readily apparent on the Queensland coast, on the northwestern coast of Western Australia similar habitat and community associations occur in a much more confused way (Marsh & Marshall, 1983). This is not the stuff that biogeographical provinces are made of and we do not believe that there is sufficient support to warrant recognition of "Banksian" and "Solanderian" faunal provinces in Queensland (*cf.* Endean, 1957).

There is no significant endemism among the corals of the eastern and western coasts of northern Australia. This group of organisms lends no support to any distinction between eastern and western faunal provinces. The differences are in the degree of coral reef formation and the physical structure of the reefs, rather than in the taxonomic composition of the faunas. All that can be said is that the coral community of northern Australia belongs to the rich central Indo-West Pacific fauna.

Coral faunas at the fringes of the Indo-West Pacific coral provinces tend to be the same species or species of the same genera (Stehli & Wells, 1971). Beyond the southern limits of coral reef development on both the eastern and western coasts of Australia, the coral fringe fauna includes species of *Coscinaraea*, *Favites*, *Favia*, *Goniastrea*, *Sympyllia*, *Plesiastrea* and *Turbinaria*. Most of the species are widespread Indo-West Pacific corals, reaching the southern limits of their range in these relatively high latitudes beyond the limits of coral reef growth. Tropical species of *Turbinaria* form large colonies and extensive communities as far east as Cape Arid on the southern coast of Western Australia, but they are not reef-forming in the strict sense. *Plesiastrea versipora* occurs around all the coasts of Australia, including the temperate south coast.

There is a handful of endemic coral species in southern Australia. *Coscinaraea macnielli* and *Scolymia australis* occur from the central western coast of Western Australia to New South Wales (the latter also at Lord Howe Island). *Coscinaraea marshae* ranges from the Abrolhos to South Australia and *Sympyllia wilsoni* from Shark Bay to Bremer Bay. These endemic southern temperate corals are certainly derivatives of the Indo-West Pacific fauna, remnants of the time when that assemblage spread into higher latitudes.

ECHINODERMS

Australian echinoderms have been relatively well studied. Although their Tertiary fossil record is not sufficiently characterized to give a temporal perspective, they are a useful group for the analysis of distribution patterns in modern shallow water species.

Northern Australia

Clark (1946) demonstrated the Indo-West Pacific character of the northern Australian echinoderm fauna. He followed Hedley's division of the northern coast into the "Dampierian Province" west of Torres Strait, and the "Solanderian Province" down the eastern coast of Queensland.

In his analysis of the northwestern fauna, Clark (1946) listed 290 species, noting an apparent high degree of endemism and close affinities with the fauna of the nearby "East Indies" area. Marsh (1976) and Marsh & Marshall (1983) have extended the list to 376 species (excluding holothurians), of which 13% are endemic. Some 66% of the species listed are shared with Indonesia, explicable by the proximity of the Indonesian island of Roti to the Australian Ashmore Reef and the favourable set of ocean currents for bringing Indone-

sian species with pelagic larvae into the Australian fauna. This especially favours coral reef species, since the shelf-edge, platform reefs and off-shore atolls of the North West Shelf "provide stepping stones" (Marsh & Marshall, 1983).

The echinoderm fauna of eastern Queensland probably includes something in excess of 300 species. Endean (1957) listed 267, excluding crinoids, and drew attention to differences between the coral reef echinoderm fauna ($\approx 35\%$ of the species) and the fauna of the soft substrates, rocky shores and fringing coral reefs of the coastal zone adjacent to the mainland ($\approx 44\%$). About 21% of echinoderm species occur in both habitats.

Rowe (1985) recognized a suite of "reef" species and a suite of "mainland" species in northern Australia. These groupings obviously have an ecological basis which is reflected also in the geographical distributions of species. The reef species tend to have wide Indo-West Pacific distributions, in keeping with the wide distribution of oceanic coral reef habitats in the Western Pacific and Indian Oceans. Rowe (1985) contended that they are the older element in the Indo-West Pacific echinoderm fauna.

In contrast, there is a strong trend towards restricted northern Australian or central Indo-West Pacific (*i.e.* "East Indies") distributions in the case of the mainland species, consistent with the development of non-coral reef or continental habitats in those regions.

Although most of the northern Australian endemics belong to the mainland group (as might be expected for species tending to be of restricted distribution), there are relatively minor differences between the mainland echinoderm faunas of the northwest and the northeast (Endean, 1957; Rowe, 1985).

According to Endean (1957) "the bulk of reef species which occur outside Australia do not occur in Australian waters west of Torres Strait", but subsequent surveys of Western Australian coral reefs have shown this to be incorrect (Marsh & Marshall, 1983). Although coral reefs are less extensive in Western Australia, the composition of their echinoderm fauna is essentially the same as the Great Barrier Reef and other Indo-West Pacific coral reef habitats.

Reef and mainland suites of species are common to both the northwest and northeast, but because of the more extensive development of coral reef habitats in the northeast the former group appears to dominate there. In our opinion, the differences are ecological and reflect different patterns of major habitat distribution within the Indo-West Pacific.

Coral reef echinoderms tend to have negatively geotaxic larvae, while the larvae of mainland (=continental) species tend to be positively geotaxic. These differences imply different dispersal capacities and may relate to the different distribution patterns (Yamaguchi, 1977).

If the reef and mainland suites of echinoderm species are treated as ecological assemblages within a regional fauna, the homogeneity of the northern Australian echinoderm fauna is apparent. Torres Strait is only a minor barrier to the distribution of either group. Nevertheless, the 13% endemism of the northeast and northwest is of moderate significance and provides some basis for treating these areas as provinces within the Indo-West Pacific Region.

In Western Australia, a significant change of habitat occurs at North West Cape. To the east of the Cape, the coastal waters are rather turbid and coral reefs tend to be poorly developed except on the shelf-break atolls far offshore in clearer oceanic waters. On the western side of North West Cape, the shelf-edge is very close to shore. Relatively high energy, oceanic conditions prevail and the coast is dominated by the Ningaloo coral reef. North West Cape is the southern

end of range for many northern Australian mainland echinoderms (Marsh & Marshall, 1983). Many reef species, however, extend to the Abrolhos.

Southern Australia

Consistent with other groups, the echinoderm fauna of temperate southern Australia exhibits a very high degree of species endemicity, probably in the order of 90% (Clark, 1946). There is significant endemicity also at the generic level, although most extant genera in southern Australia have the majority of their species in the Indo-West Pacific Region. Rowe & Vail (1982) estimated that more than 70% of the Tasmanian species are derived from tropical stock. These tropical elements in the fauna are derivatives of the early Tertiary fauna of Tethys. The remainder have cold water affinities and may be regarded as relicts of the early Tertiary Palaeoaustral fauna.

About 22% of Tasmanian echinoderm species also occur in New Zealand (Rowe & Vail, 1982). Most of these species belong to the cold water element. Ten species common to Tasmania and New Zealand are not found on the shores of the Australian mainland. Several species (such as *Psilaster acuminatus*, *Coscinasterias calamaria*) are common to southern Australia, New Zealand and South Africa and there are some cosmopolitan species (for example *Echinocardium cordatum*). Whether these echinoderms owe their wide range to ancient common origins or recent trans-oceanic dispersal is a matter for further study. Edgar (1987) suggests that trans-Tasman dispersal from Australia to New Zealand may be common and is consistent with current direction and rate of flow, but that migration in the reverse direction is unlikely.

Some of the cold water echinoderm genera represented in southern Australia, such as *Patiriella*, *Asterodon*, *Calvasterias*, *Astrostole* and *Pseudechinus*, are circumpolar, or partly so, in the Southern Ocean (Knox, 1979). The distributions of these genera were interpreted by Fell (1962) in terms of West Wind Drift dispersal. Noting that the majority of species in such genera tends to be at the western end of the circumpolar range (Fig. 3.12), Fell inferred that the original source lies there with eastern representations derived by means of clockwise dispersal of pelagic larvae or epiplanktonic adults. Edgar (1987) discusses this process for a variety of marine plants and animals. Knox (1979) pointed out that in the early Tertiary, the coastlines of Australia, New Zealand, Antarctica and South America were continuous and that common elements in the modern echinoderm faunas of the higher latitudes of these areas are to be expected. He argued that larger numbers of species could result from larger areas and opportunities for speciation (as in the case of southern Australia) and need not necessarily indicate centres of origin. Nevertheless, whatever the point of evolutionary origin, West Wind Drift dispersal appears to be an important factor in the distribution of Southern Ocean echinoderms.

Rowe & Vail (1982) analysed the distribution of Tasmanian echinoderm species and found three common patterns. A General Southern Group, comprising almost half the total fauna, ranges across the entire southern coast and northwards up the coast of New South Wales in the east and the central western coast of Western Australia. A Southwestern Group ranges from Tasmania westward into southern Western Australia. A Southeastern Group extends from Tasmania northward up the coast of New South Wales. Many of these species overlap in the Bass Strait area. Most of the Tasmanian species shared with New South Wales are found on the northern and eastern coasts of Tasmania, whilst those shared with the south and west are confined to the northern Tasmania coast. The southern endemic genera show similar patterns

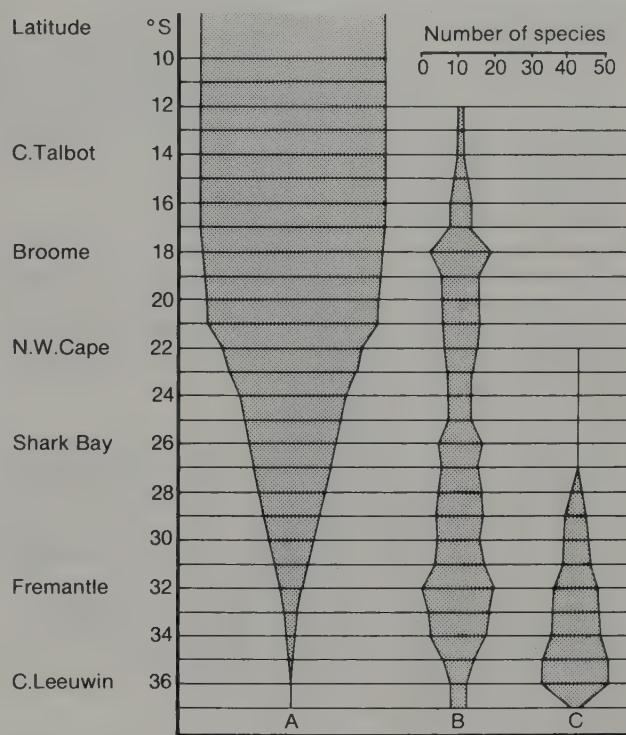


Figure 3.12 Latitudinal distribution of Western Australian Asterioidea; A: species with an extra-Australian distribution to the north; B: species endemic to Western Australia extending into the Northern Territory and South Australia; C: species with a southern Australian distribution including two species whose range extends to New Zealand. (After Marsh, 1976)

(Rowe & Vail, 1982) with a General Southern Group, a Southwestern Group and a Southeastern Group, each accounting for about one-third of the total number of endemic genera.

Marsh (1976) clearly demonstrated latitudinal attenuation of the tropical and temperate asteroid faunas on the western coast (Fig. 3.12), with no sharp boundary between them and an overlap of northern and southern species between North West Cape and Cape Leeuwin. Tropical species are represented strongly in deeper waters off the mid-western coast (more so than in the shallows), but few pass around Cape Leeuwin. Many of the southern species which extend northwards beyond Cape Leeuwin also range up the eastern coast of New South Wales and equate to the General Southern Group of Rowe & Vail (1982). Another group ranges only from Shark Bay into South Australia and equates to the Southwestern Group. A significant result from Marsh's (1976) analysis is the discovery of 10 asteroid species endemic to the western coast overlap zone (Fig. 3.12).

There is no equivalent analysis of eastern coast (*i.e.* Peronian) Australian echinoderms although Clark (1946) indicated that a similar situation exists there as on the western coast. There is an overlap of northern (tropical) and southern (temperate) species, a group of southern species widely distributed across southern Australia and a group of species endemic to the area, *i.e.* the Southeastern Group of Rowe & Vail (1982).

These echinoderm data support the generally accepted notion of a distinctive southern Australian marine fauna, with Bass Strait and Cape Leeuwin marking positions within the region where significant changes in faunal composition occur. Endemism in Tasmania is relatively minor and there is little evidence to support the concept of a cool temperate Maugean Province.

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CONCLUSION

From this analysis of selected marine taxa emerge consistent generic and species distribution patterns which we believe are representative of the entire shallow water marine fauna of Australia. The major underlying scenario is that two ancient faunas of different early Tertiary origins have contributed to its modern composition.

The pan-tropical Tethyan fauna and its successor, the modern Indo-West Pacific fauna, have dominated the northern coast of Australia since the beginning of the Tertiary. They also have contributed strongly, especially in the southwest, to the temperate marine fauna which has evolved in southern Australia since the middle Tertiary.

The ancient temperate Palaeoaustral fauna of southern high latitudes and its southeastern Australian derivatives have dominated the southeastern corner of Australia, also since the early Tertiary. The fortunes of this element have waxed and waned during that period, as latitudinal position, climate and ocean currents have varied. The southeastern Indian Ocean arm of the Indo-West Pacific fauna which protruded onto the southern coast of Western Australia through much of the Tertiary has since contracted to the west and north and the modern southeastern Australian fauna has expanded westwards to dominate the entire southern coast.

The high degree of endemism in the marine fauna of the southern coast of Australia has ancient and profound origins. The northern coast of Australia, therefore, is part of the vast Indo-West Pacific Faunal Region, while the southern coast may be regarded as a distinct faunal region in its own right, the Southern Australian Region.

Indo-West Pacific Region (Northern Australian Zone)

One of the most striking features of world marine animal distribution patterns is the extraordinary species-richness of the central part of the Indo-West Pacific, a feature common to almost every group. The coast of northern Australia is part of that high diversity centre.

The tropical marine fauna of northern Australia is remarkably uniform and widespread Indo-West Pacific species dominate. Nevertheless, there are faunistic differences between east and west and some groups, especially those in which planktonic larval capacity is limited or lacking, exhibit a degree of endemism (as much as 13%). On the eastern coast of Queensland there is a western Pacific element not present on the North West Shelf. Conversely, on the North West Shelf a number of species is shared with the Indian Ocean and the Indo-Malay Archipelago but not with Queensland. Both the northeast and northwest have endemic elements. The northeastern endemics tend to be confined to the Great Barrier Reef and the Queensland coast south of Torres Strait or to some part thereof. The majority of the northwestern endemics is centred on the North West Shelf between Darwin and North West Cape, but some extend eastwards to Torres Strait and southwards onto the central western coast of Western Australia. Torres Strait, Darwin and North West Cape are localities within the Northern Australian Zone where many species end their range.

Some of the differences between the northeastern and northwestern faunas may be explained in ecological terms, *i.e.* the greater development of coral reef habitats in the northeast. Clearly, however, historical factors also are involved. Following the early Tertiary impingement of the Australian Plate upon Southeast Asia, but prior to the late Pleistocene flooding of the shelf area between New Guinea and Australia, the North West Shelf and the eastern Queensland Shelf must

have been relatively isolated from each other. Some of the differences between the northwestern and northeastern faunas in present times and the closer affinities between the non-coral reef faunas of the North West Shelf and Indonesia, may be accounted for by that long period of isolation.

Beyond Shark Bay (26°S) in the west and Sandy Cape (25°S) in the east, there begins an attenuation of the tropical fauna and the progressive replacement of tropical species with temperate ones within the western and eastern overlap zones. Actually, many tropical (especially mainland suite) species fail to pass south of North West Cape because of an abrupt ecological change there. Replacement of tropical with temperate species, however, does not begin before Shark Bay. The northern boundary of the western transition zone is better placed in that latitude rather than at North West Cape.

The Houtman Abrolhos Islands off the western coast and Lord Howe Island off the eastern coast are southerly outliers of the tropical fauna by reason of their positions in the path of warm southerly flowing currents, the Leeuwin and East Australia Currents, respectively.

A feature of species distribution patterns of many northern tropical groups is the presence of two suites of species with different habitat requirements and different distribution patterns within the Indo-West Pacific Region.

Coral-reef inhabiting species tend to be distributed widely throughout the region. They have been referred to as "oceanic" species by Abbott (1960) and "reef" species by Endean (1957). Those with relatively short generations (such as strombs and cowries among the gastropod molluscs) tend to be polytypic and such groups commonly exhibit endemism at the peripheries of the region. Those with long generation periods (corals) tend to be subject to intra-population variation, but are rarely geographically polytypic.

The second suite includes species which inhabit the nutrient-rich shores of continents or well-vegetated continental islands. These species tend to have restricted distributions, often limited to the central part of the Indo-West Pacific Region (the Indo-Malay Archipelago and northern Australia). They have been referred to as "continental" species (Abbott, 1960) and "mainland" species (Endean, 1957).

The North West Shelf, where the continental type of habitat predominates, has a preponderance of continental species, although recent surveys of shelf-edge coral atolls have shown that coral reef species are represented more strongly in the western fauna than once thought. In eastern Australia, where both continental and coral reef habitats are well developed, there is a higher number of reef species.

Naturally, reef species tend to have a capacity for wide dispersal, usually by means of planktotrophic larvae, since they must be able to cross wide zones of uninhabitable deep ocean. Continental species need not necessarily have this capacity. Groups such as the volutid gastropods, which have no pelagic larvae, are almost invariably continental.

Southern Australian Region

Almost every group of marine animals in southern Australia exhibits very high species endemism (usually over 90%). The level of generic endemism varies between groups, but is highest in southeastern Australia. Some endemic genera are relicts of groups once distributed widely in Tethys or derived from these. Others have a long history in southeastern Australia and have their origins in palaeoaustral ancestors.

Many southern Australian endemic species are confined to the southern coast between Cape Leeuwin and Bass Strait (Fig. 3.13). Many range across the southern coast and up

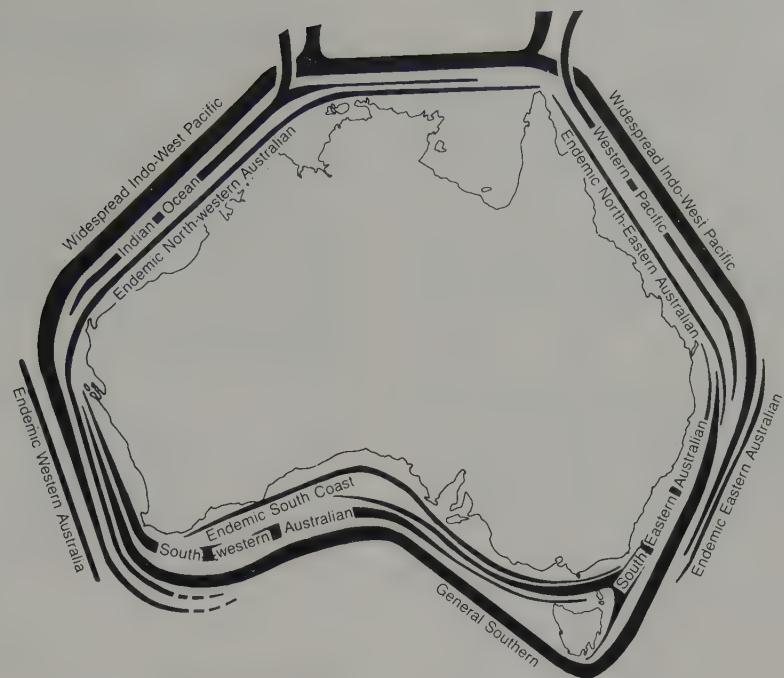


Figure 3.13 Common distribution patterns of shallow water benthic animals on the Australian coast, showing approximate boundaries of the Indo-West Pacific Region (northern Australian sector) and Southern Australian Region and the wide Eastern and Western Overlap Zones between them.

both the western and eastern sides of the continent and are common to the southwest and southeast ("General Southern distribution" Fig. 3.13). But, significant numbers of species in many different taxa are centred in the southwest or the southeast (Fig. 3.13). The former group is characterized by species of Tethyan origin while the latter is characterized by southeastern Australian-Palaeoaustral derivatives. In both groups, a proportion of the species is confined to the central west or central east coasts, respectively (*i.e.* the western and eastern overlap zones), but a majority extend their range onto the southern coast. The two groups tend to overlap on the coast of South Australia (Fig. 3.13).

An important element in the southern fauna is the group of species which has circumpolar, or partly circumpolar distributions in the Southern Ocean. These tend to be species with planktotrophic larval or epipelagic adult dispersal capacity and are assumed to owe their distribution patterns to the West Wind Drift. They are most conspicuous in the southeast of Australia which penetrates into relatively high latitudes and the path of this current.

There are several southern Australian temperate species of diverse groups which also occur in similar latitudes in the northern Pacific or which have close relatives there. Some of them (for example *Mytilus edulis*) are both circumpolar and bipolar. The mechanism by which these species "jumped the equator" is yet to be adequately explained, but the event is generally assumed to have occurred when the tropical zone was constricted.

The marine fauna of Tasmania is of particular interest. Many writers have claimed that Bass Strait and Tasmania warrant distinct status as a "cool temperate" province (Maugean). There is little support for this in the fauna itself, if endemism is the criterion. Although the widely distributed Southern Ocean species are represented most strongly in this region, they represent only a small part of the total fauna there. The dominant elements are the south coastal and General Southern species. Several authors, writing about different groups, have noted that southeastern species tend to be

common on the east coast of Tasmania, presumably because of the effects of the East Australia Current, while southwestern species tend to be common on the northern coast.

The northern boundaries of the Southern Australian Region may be located approximately at Cape Howe in the east and Cape Leeuwin in the west. Beyond these points, the attenuation of the southern fauna begins and the temperate species are replaced progressively by tropical ones. Although these localities do mark the ends of range of many species, however, many more transgress and these localities should be regarded only as convenient points for zoogeographical classification purposes.

The Overlap or Transition Zones

As their names imply, the Western and Eastern Overlap Zones are long north-south stretches of coast where the tropical Indo-West Pacific fauna of the north and the temperate southern Australian fauna of the south comingle. They are dynamic zones which have shifted their latitudinal positions in the past as climates and currents have varied. Within them, many individual species are subject to extension and contraction of range even on relatively short time-scales. They exist by reason of southerly-flowing warm currents (Leeuwin and East Australia Currents) which are seasonally inconsistent in these zones.

At present, the boundaries of these zones may be located at Shark Bay and Cape Leeuwin (western zone) and Sandy Cape and Cape Howe (eastern zone). Although both western and eastern overlap zones are characterized by a mixture of tropical and temperate species, both have a significant number of endemic species. The western ones have mainly Tethyan or Indo-West Pacific affinities, while the eastern ones generally have autochthonous origins or Palaeoaustral ancestors.

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Zoogeographical Provinces

Conventionally among biogeographers, areas which have distinctive faunas and floras may be designated as distinct, biogeographic regions or provinces. The Australian coastline has been divided in this way (Fig. 3.1). There can be no doubt that northern and southern Australia support marine faunas of very different origins and history and that they belong to distinct faunal regions. Within the northern and southern regions, distinctive faunal elements may be recognized and related to historical as well as ecological causes. Some find it convenient to formalize these concepts as named faunal provinces.

In the northern Australian sector of the Indo-West Pacific Region, the high endemism of the North West Shelf fauna is acknowledged by referring to that area as the "Damperian Province" with its boundaries at about Geraldton on the west coast and Torres Strait in the northeast. Mainland Queensland has been designated the "Banksian Province" and the Great Barrier Reef area the "Solanderian Province". The distinction is mainly ecological. The whole of the eastern Queensland coast now is commonly referred to as the "Great Barrier Reef Province".

In the Southern Australian Region, the distinctive southwestern elements of the fauna are used as a basis for designating the area from Geraldton to western Bass Strait as the "Flindersian Province". Although there is ample evidence that the faunas of these parts of the coast do have different elements with different origins, formal designations of provinces ignore the large number of General Southern and

southern coastal species which are common to both areas and the fact that many of the southeastern or so-called "Peronian" species range into western Victoria or South Australia (Fig. 3.13).

Recognition of a cool temperate "Maugean Province" for Bass Strait and Tasmania rests more on ecological groupings of rocky shore faunas than on any historical evidence or a significant degree of local endemism.

The problem with these classifications is that the location of the boundaries between the provinces varies according to the group of organisms studied and that there is so much overlap that exceptions outnumber the species which obey the rules. Whether or not one chooses to use the biogeographical provinces depends on whether emphasis is to be placed on the similarities or the differences.

Of paramount importance is the recognition of the different origins of elements in the modern fauna, the reconciliation of those differences in historical terms and the blend of that perspective with ecological knowledge to explain present distribution patterns.

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4. THE PRESENT AUSTRALIAN ENVIRONMENT - TERRESTRIAL AND FRESHWATER

P. B. BRIDGEWATER

INTRODUCTION

Interactions between organisms and their physical surrounds (environment) produce an ecological mosaic recognized as landscape. Over large continental areas, differences in macroclimate are reflected in landscape differences which biogeographers have termed biomes, life zones or formations. Rowe & Sheard (1981) note that landscapes can be "most efficiently apprehended through such features as landform and water-form that control flux regimes or through such indicators as biota and soil that equilibrate rapidly to flux changes". They also note that "the landscape is conceived as a grouping of ecosystems, large and small, nested within one another in a hierarchy of spatial sizes".

With its presently used ambiguous and vague connotations, "ecosystem" appears increasingly an inappropriate term for precise communication. Naveh & Lieberman (1983) argue that "ecosystem" is more properly defined as a "landscape unit". Landscape can be given a precise definition as:

"a part of the space on the earth's surface, existing as a complex of systems, formed by the activity of rock, water, air, plants, animals & man and that by its physiognomy forms a recognizable entity" (Zonneveld, 1979).

Following these trends, this Chapter describes the environmental setting of Australia within the framework of the natural regions defined by Barlow (1985), after discussing general aspects of climate, geology, soils, vegetation and fire in Australian landscapes. As this and future volumes of the *Fauna of Australia* will have numerous detailed examples of environmental effects on the fauna, this Chapter is confined to a discussion of the environment *per se*.

CLIMATE

In Australia, climate exerts a major control over the distribution of biota through direct and indirect effects. These effects may take a wide range of form. For most of the fauna, climatic effects are filtered through at least the vegetation component of the environment. Nevertheless, animals which are not well adapted to extreme cold conditions, for example, are limited in their ability to colonize the high alpine and southern inland frost-frequent areas.

To understand climatic factors critical for biota a sense of the historical development of the environment is needed. Frakes *et al.* in Chapter 1 outline many of the processes by which Australia has arrived in its present location and with its present climates.

Nix (1982) argues that temperature is important in terms of organism distribution. In a well-argued paper he uses the terms megatherm, mesotherm and microtherm to define explicitly biogeographic regions. Linked with a growth index, combining light, thermal and moisture regimes, he recognizes three major regions with two interzones. He categorizes these as:

1. Megatherm seasonal (Torresian)
2. Megatherm mesotherm arid (Eyrean)
3. Mesotherm microtherm seasonal (Bassian) with interzones between 1 & 2 and 2 & 3. Parts of the northeast coast are characterized as megatherm non-seasonal (Irian). Terms in parentheses are those of Schodde & Calaby (1972).

Climate is linked with many other factors. For example, an area typically well-watered but suffering from a period of dry years may suffer devastating effects from drought with the possibility of holocaust wild-fires considerably increased. Similarly, areas receiving heavy rainfall, particularly at an unusual time of year, may suffer a range of environmental effects. Some species may be particularly adapted to take advantage of these environmental peculiarities.

An example, the River Red Gum (*Eucalyptus camaldulensis*) is found frequently along the banks of inland rivers and creeks. Whenever major flooding occurs, a new band of *E. camaldulensis* develops at the floodline. Many of these seedlings may die, but some become established and, through sediment deposition, aid the development of new banks. Elsewhere death of older trees increases the potential for erosion of existing banks. In this way new creeks form and new opportunities for all biota are opened up.

The development of the Ophthalmia Dam on a branch of the Fortescue River in the Pilbara region of northwestern Australia has exemplified these effects. In that region, *Eucalyptus camaldulensis* and *E. coolabah* are confined in narrow bands along the edges of the rivers and anastomosing side creeks. After cyclonic or heavy rain events, a "lake" of varying depth is created behind the dam wall.

Because the "lakes" have varying shorelines, a fringing forest of both of these species has now become established. Although too early at this stage to ascertain how many of these young trees will survive to maturity, the newly created woodland offers enhanced biological opportunity for a range of organisms. While this sequence of events arises from human activity, the suggestion is that natural effects are able to promote sudden ecological or geographical range extensions for particular species or communities.

An average climate for Australia may be estimated. Climate measurements for approximately 2,700 spatial points across the surface of Australia were estimated using BIOCLIM (Nix, 1986). These points are in the grid cells formed by the intersections of 0.5° latitude and longitude grid lines. Averaging these measurements, the mean annual temperature is 21.5°C and the annual average rainfall is 451 mm (J. Busby, pers. comm.). Over half of that rain falls in the warmest quarter of the year with only 41 mm falling in the coldest quarter. While these figures are clearly a gross simplification of the Australian climate, they allow several interesting generalizations:

- a. this average climate is tropical-seasonal;
- b. climates such as the pronounced winter-rain region of southwestern Australia and the non-seasonal climates of southeastern Australia and Tasmania differ widely from the

4. PRESENT ENVIRONMENT

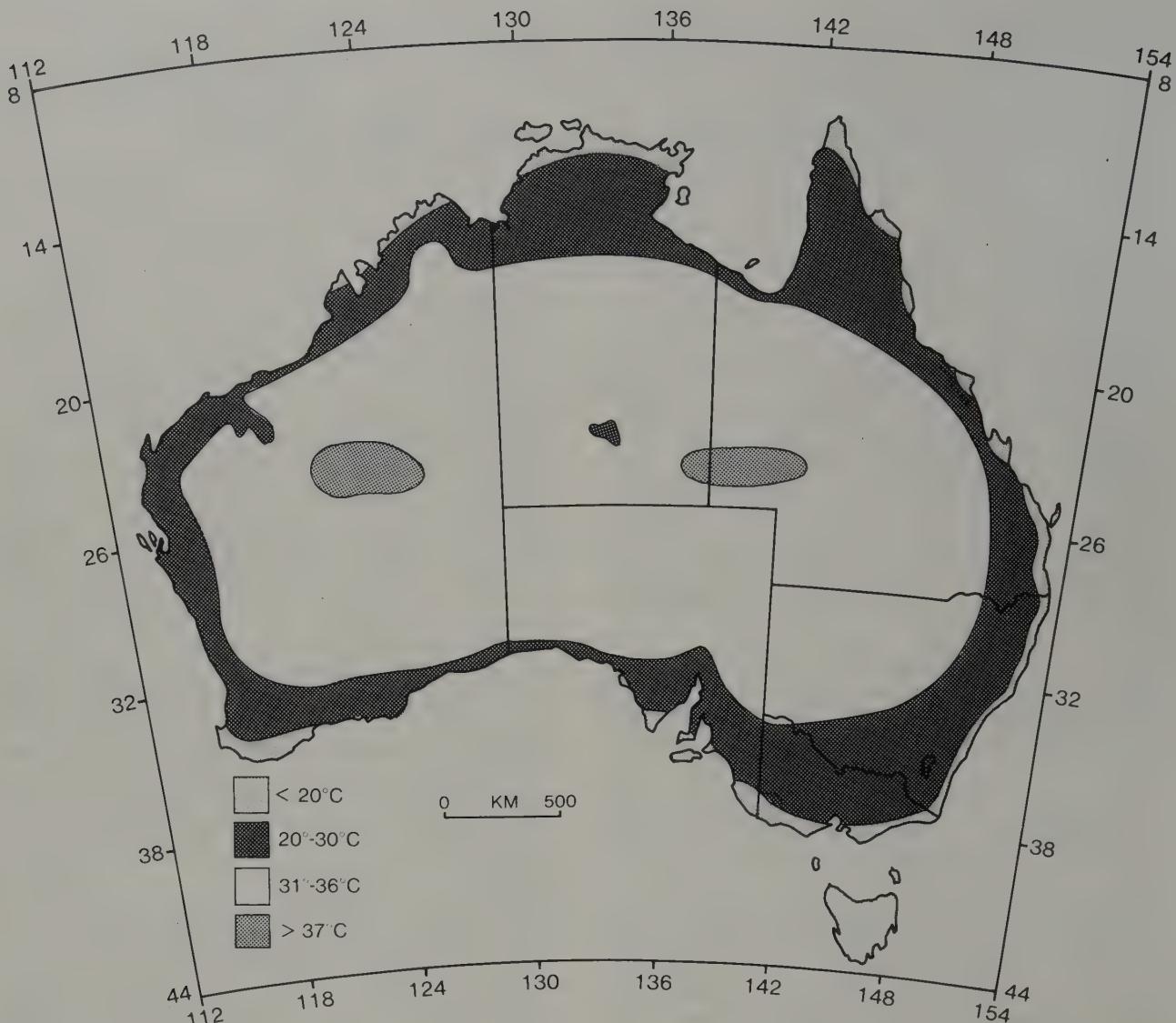


Figure 4.1 Variation between mean annual maximum temperature and mean annual minimum temperature. (From Bureau of Meteorology data)

"average" climate of the continent;

c. although Australia has a number of areas with very high rainfall (northeastern Queensland, western Tasmania), these differ widely from the average rainfall noted above.

In the central part of Australia cyclones which cross the eastern, northern and western coasts of Australia act as influences on the biota. Because cyclones are unpredictable in their frequency and their likely trajectory, no estimate can be made of the climate of much of central Australia on an annual basis. Purdie (1984) notes:

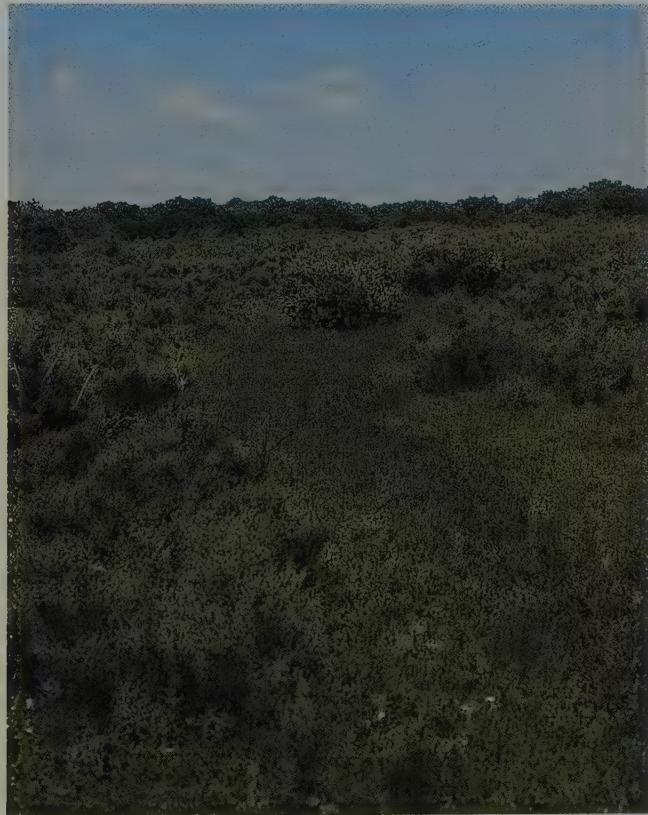
"The cycles of fire and drought/wet have probably operated for thousands of years, and still maintain the vegetation in a dynamic state resulting in spatial and temporal heterogeneity of community structure and composition which are not apparent at a single place or time."

Results of such a rapid perturbation in an otherwise steady-state system are reflected in a dramatic change of landscape texture (patterning). This change is effected by the filling of ephemeral water-courses and lakes and mirrored by ephemeral populations of plants and animals which persist only when conditions are favourable. Seasonality and the amount of the rainfall will determine which organisms develop and

their level of persistence, e.g. Mott (1973). Whichever ephemeral plant community is produced, it is within the structural framework provided by the perennial communities.

Figures 4.1 and 4.2 show variation in expected annual rainfall and annual temperature ranges. The areas which appear most "stable" are near coastal regions of southwestern and southeastern Australia. These regions have the most assured continuity of rainfall (on an annual basis) and the least annual temperature range. As discussed above, these regions also diverge most widely from the average climate. In contrast, the wide band of the continent running from the coast of northwestern Australia southeast through central Australia shows a very wide annual temperature range and a very unpredictable (and low average) annual rainfall. This climatic uncertainty has a major role to play in the spatial variability and richness of arid Australian flora and fauna, particularly the ephemeral elements.

European settlers often tend to see the climate through eurocentric eyes, whereas Aborigines often have a more detailed interpretation of climatic variability. Chase & Sutton (1981) point out that Aboriginal tribes in a range of regions across northern Queensland recognized between five and six distinct climatic periods throughout the year. These divisions

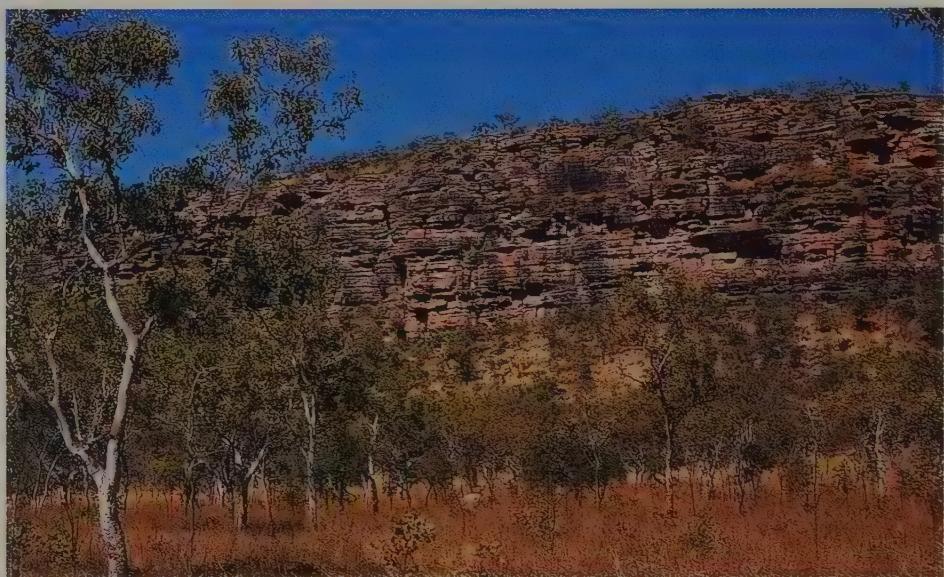


1 & 2 Examples of southern coastal salt marsh from Western Port Bay, Vic. Coastal salt marsh in southern Australia is dominated by shrubby succulent species, with occasional grassy flats.



3 Estuarine vegetation in tropical Australia is formed from species of mangroves. Mangroves are shrub or tree species belonging to a range of families. This photograph shows *Rhizophora stylosa* (with stilt roots) and the shrub *Aegialitis annulata* in the foreground. A creek edge near Port Headland, W.A.

Photographs: P.B. Bridgewater



Five photographs on this and facing page show aspects of woodland vegetation in the wet-dry tropics.

4 A filled creek in the wet season surrounded by *Melaleuca* thicket.
Magela Creek, Kakadu National Park, N.T.

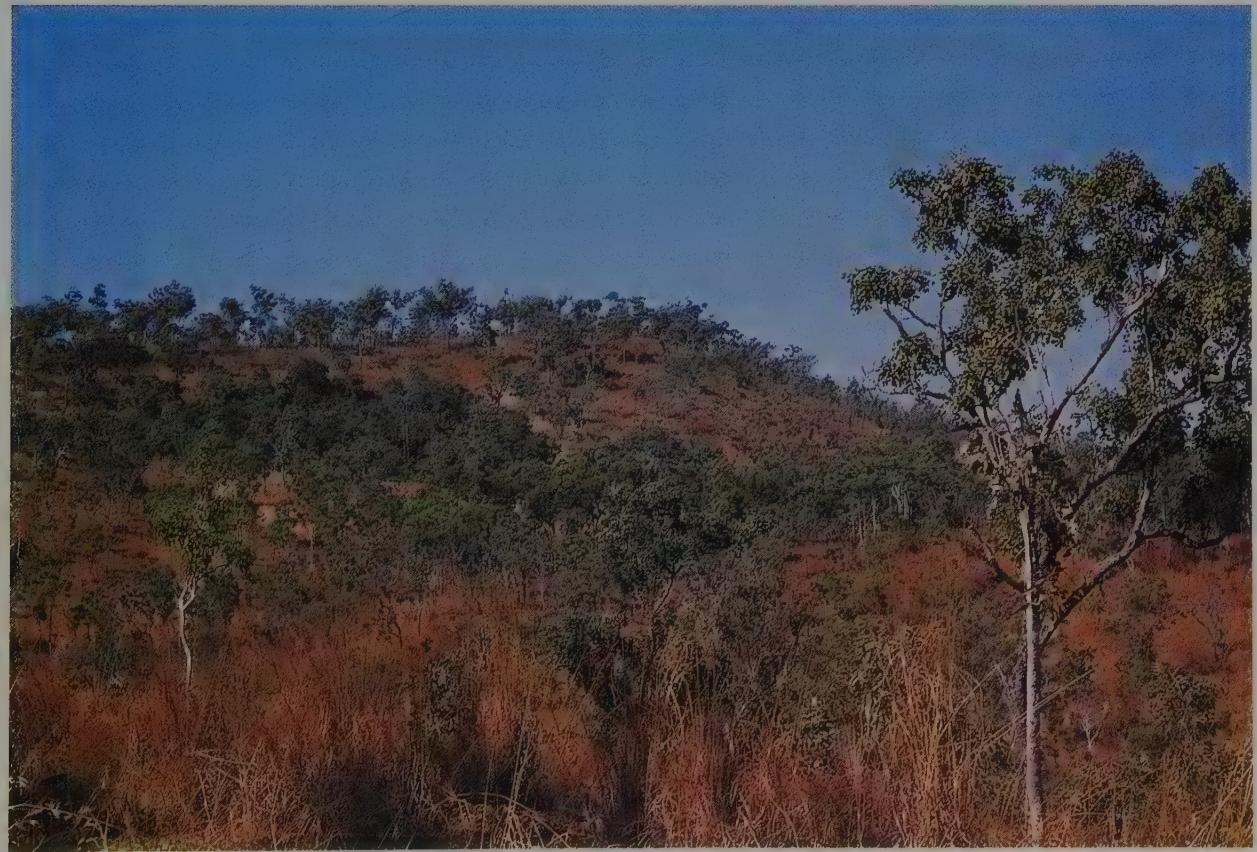
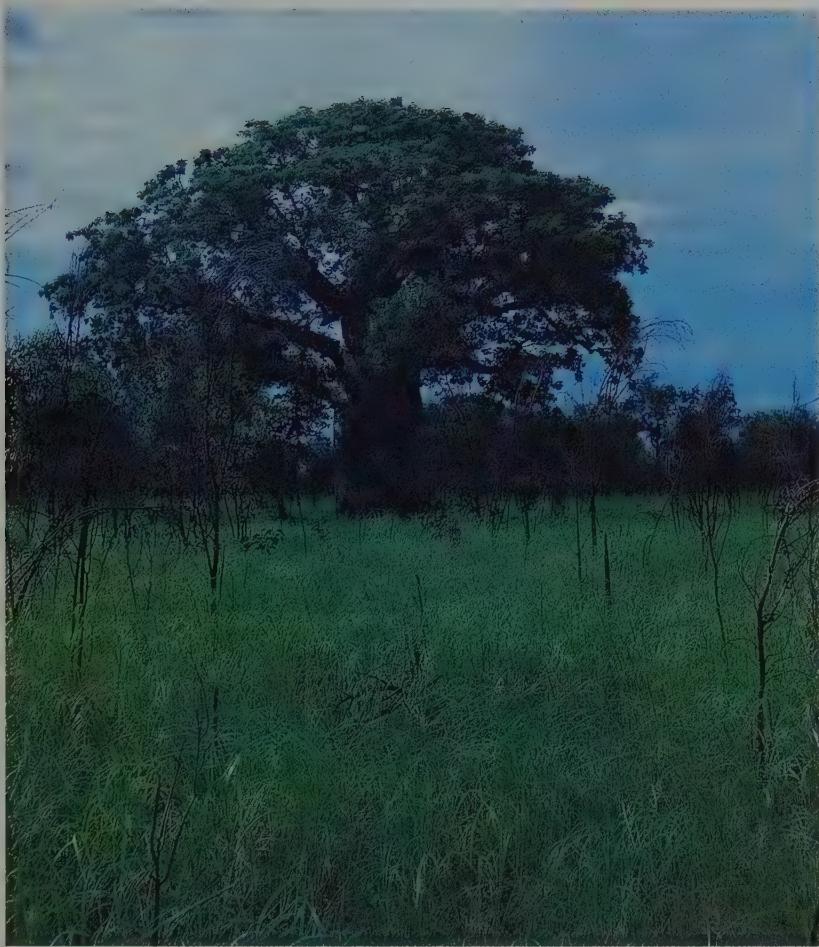
Photograph: R.C. Longmore

5 "Eudesmia" - "Corymbia" - "Blakella" - "Sympyomyrtus" woodland near the Carson Escarpment, Kimberley, W.A. dominated by eucalypts. Dry season aspect, showing grass understorey.

Photograph: A.S. George

6 "Eudesmia" - "Corymbia" - "Blakella" - "Sympyomyrtus" woodland near Somerset, N Qld showing dominance by eucalypts and *Livistona*. Dry season aspect, recently burnt.

Photograph: R.C. Longmore



7 "Eudesmia" - "Corymbia" - "Blakella" - "Symphyomyrtus" woodland with *Adansonia gregorii* (Baobab tree). Near Broome, W.A. Wet season aspect with living grass understorey and evidence of shrubs burnt in the last dry season. Photograph: P.B. Bridgewater

8 "Eudesmia" - "Corymbia" - "Blakella" - "Symphyomyrtus" woodland with eucalypts and *Erythrophleum* dominant - Mitchell Plateau, W.A. Dry season aspect. Photograph: A.S. George



Photographs on this and following page showing tropical and subtropical rainforest.

9 Typical buttress roots and lianes in rainforest from Iron Range, northern Qld.
Photograph: R.C. Longmore

10 Subtropical rainforest showing dense canopy of mixed tree species from Cunningham's Gap, Qld.
Photograph: R.C. Longmore



11 Epiphytes, typical of rainforest, are prominent in this photograph from Iron Range, northern Qld. Photograph: R.C. Longmore

12 *Archontophoenix* sp. in complex notophyll vine forest, Bellangry State Forest, N.S.W. Photograph: G.R. Dyne



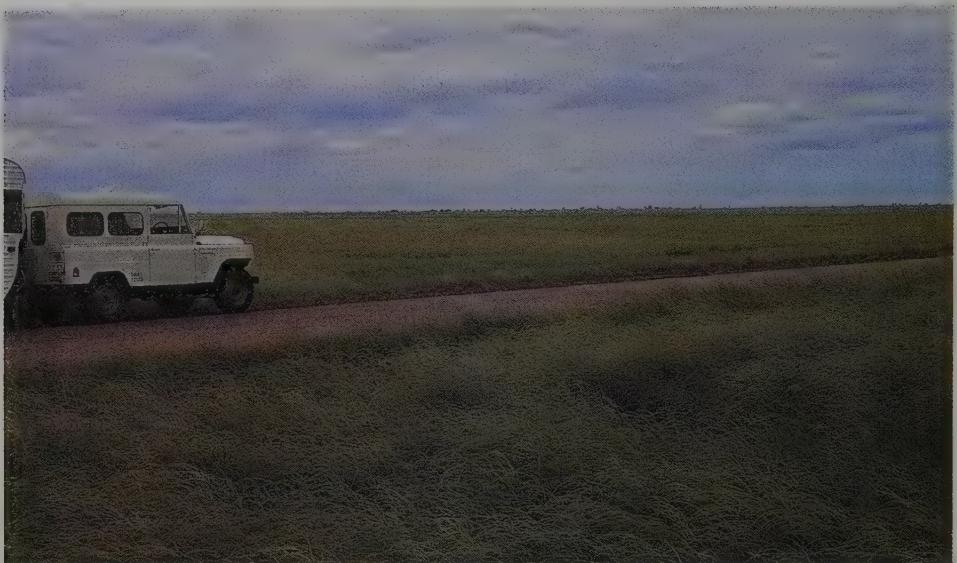
13 General view of forest in Bunya Mountains National Park, Qld. This shows "Symphyomyrtus" - "Monocalyptus" forest on the ridges and four slopes, with multi-species rainforest in the gullies.

Photograph: P.B. Bridgewater



14 Rainforest edge - Bunya Mountains National Park, Qld. Rainforest in this region is dominated by conifers, especially *Araucaria bidwillii* (right) and *A. cunninghamii* (left). Tops of ridges in this park do not carry forest, but are grassy "balds", often with *Xanthorrhoea johnsonii* present.

Photograph: P.B. Bridgewater



15 Barkley Tableland, N.T. Late wet season, showing *Astrebla* grass-
land.
Photograph: A.S. George

16 Grassland/woodland interface in south central Qld. Late spring.
Photograph: R.C. Longmore

17 *Acacia shirleyi* woodland northern Qld, developed on laterite
overlying sandstone. This is a scattered vegetation type across north-
ern Australia.
Photograph: A.D. Chapman



18 Hamersley Range, near Mt Tom Price, northern W.A. Slopes carry hummock grassland of *Triodia* spp. with an open tree layer of eucalypts.
Photograph: A.S. George



19 Hamersley Range, near Newman, W.A. Two species of *Triodia*, with *Eucalyptus leucophloia* in the creekline. Foreground is *T. bas-
dowii* with *T. pungens* towards the creek.
Photograph: P.B. Bridgewater

Tropical / Subtropical evergreen wooded vegetation

- 1 "Eudesmia" — "Corymbia" — "Blakella" — "Sympyomyrtus" forest or woodland
- 2 "Corymbia" — "Blakella" — "Sympyomyrtus" woodland
- 3 Acacia woodland
- 4 Melaleuca shrubland
- 5 "Corymbia" — "Sympyomyrtus" woodland
- 6 "Sympyomyrtus" — "Monocalyptus" forest
- 7 Angophora — "Eudesmia" — "Corymbia" — "Blakella" — "Sympyomyrtus" woodland
- 8 "Monocalyptus" — "Sympyomyrtus" — "Idogines" forest
- 9 "Corymbia" — "Sympyomyrtus" — "Gaubea" forest
- 10 Tropical rain forest
- 11 Subtropical rain forest
- 12 Tidal (mangrove) forest

Semi-arid grassland and shrublands

- 13 Dichanthium grassland (blue grass)
- 14 Astrebla grassland (mitchell grass)
- 15 Zygochloa grassland (cane grass)
- 16 Triodia grassland with an open tree layer of Acacia, Allocasuarina or Eucalyptus
- 17 Atriplex — Maireana semi-succulent shrubland (saltbush)
- 18 "Eudesmia" — "Monocalyptus" — "Sympyomyrtus" sclerophyllous shrubland (mallee)
- 19 Acacia shrubland (mulga)
- 20 Acacia thicket, with Triodia understorey

Temperate forests, grasslands and shrubland

- 21 "Corymbia" — "Monocalyptus" — "Sympyomyrtus" forest
- 22 "Sympyomyrtus" woodland, with scattered shrubs understorey
- 23 "Sympyomyrtus" woodland, with shrub or grass understorey
- 24 "Sympyomyrtus" woodland, with Bothriochloa / Heteropogon understorey
- 25 Stipa grassland
- 26 "Monocalyptus" woodland *
- 27 Alpine sclerophyllous shrubland
- 28 "Sympyomyrtus" — "Monocalyptus" forest
- 29 "Corymbia" — "Sympyomyrtus" — "Monocalyptus" winter-rain forest
- 30 "Sympyomyrtus" winter-rain sclerophyllous forest
- 31 Banksia — "Corymbia" — "Monocalyptus" woodland
- 32 Proteaceae — Myrtaceae — Mimosaceae — Epacridaceae shrubland
- 33 Nothofagus rain forest
- 34 Gymnoschoenus sedgeland



* Mapped areas may include Alpine sclerophyllous shrubland on the higher peaks

POTENTIAL NATURAL VEGETATION





20 Distant view of the Olgas, N.T., central Australia. Mixed grassland in foreground, with *Acacia aneura* shrubland mid-distance.

Photograph: A.S. George

21 Open groves of *Allocasuarina decaisneana* on red sand dunes, near Sir Frederick Range, W.A.

Photograph: A.S. George

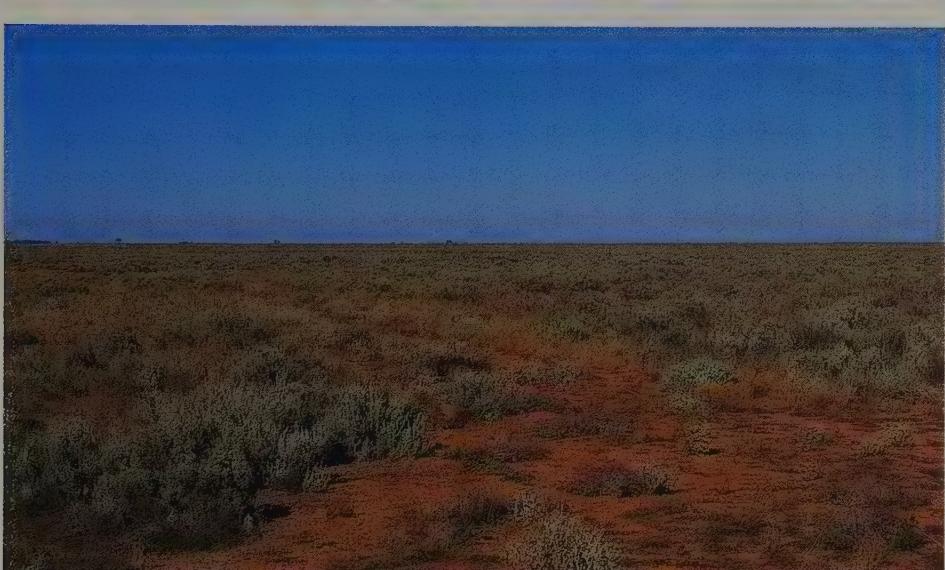
22 *Acacia* shrubland, near Hamelin Pool, central coastal W.A. Ground cover of ephemeral species, especially *Cephalipterum drummondii*, developed after above-average rains.

Photograph: A.S. George



23 *Acacia* shrubland north of Laverton, W.A. Ground flora with few ephemerals especially *Waitzia* and *Helipterum*.

Photograph: A.S. George



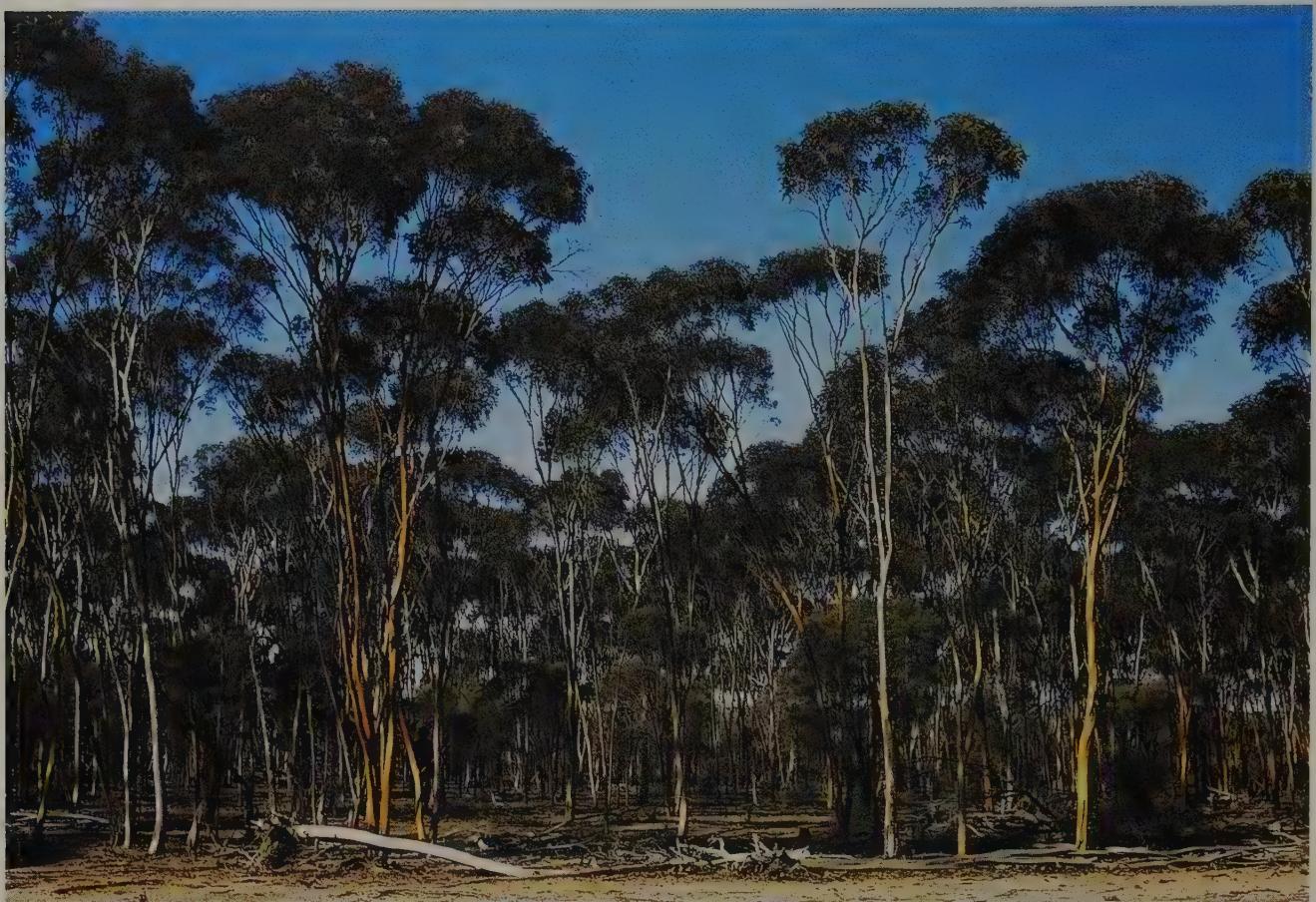
24 *Atriplex* - *Maireana* semi-succulent shrubland northwest of Deniliquin, N.S.W.

Photograph: P.B. Bridgewater



25 *Atriplex* - *Maireana* semi-succulent shrubland with abundant grass understorey (chiefly *Eragrostis*). Between Tibooburra and Broken Hill, N.S.W.

Photograph: R.C. Longmore



26 An example of "Symphyomyrtus" woodland, dominated by *Eucalyptus flocktoniae* and *E. salubris* near Kulin, W.A. In such woodlands the ground layer may be extremely sparse or dominated by low shrubs or grasses.

Photograph: A.S. George



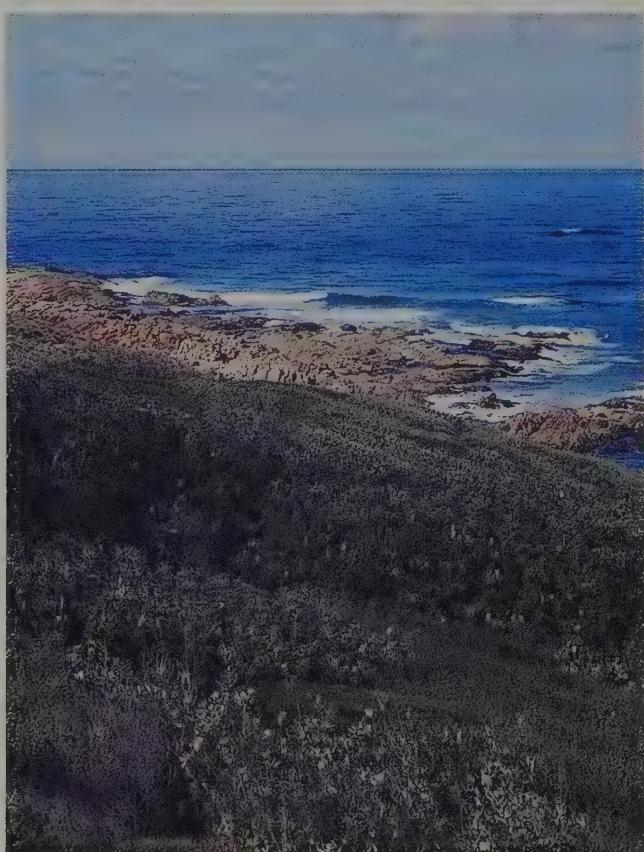
27 Aerial view of salt lakes near Pingrup, W.A. This scene is typical of inland southern W.A. where much of the vegetation has been cleared for agriculture, leaving only narrow corridors of vegetation.

Photograph: A.S. George



28 "Symphyomyrtus" - "Monocalyptus" forest - dominated by *Eucalyptus delegatensis*. This is typically referred to as an example of "wet sclerophyll" forest. The subalpine regions of Brindabella Range, A.C.T.
Photograph: R.C. Longmore

29 "Symphyomyrtus" - winter rain sclerophyll forest - dominated by *Eucalyptus diversicolor* forest. Another forest type referred to as "wet sclerophyll", from the higher rainfall regions of southwestern W.A.
Photograph: P.B. Bridgewater



30 Low shrubland (often referred to as heathland) from coastal dunes near Israelite Bay, W.A. This vegetation is dominated by many different species. Prominent flowering shrubs include *Acacia* and *Pimelea*.

Photograph: R.J. Hnatiuk

31 Stunted shrubland near Wingin Inlet, Vic. dominated by wind-pruned *Banksia integrifolia* – normally a tree species.

Photograph: P.B. Bridgewater

32 Tall shrubland dominated by *Banksia ornata* and the mallee form of *Eucalyptus baxteri* – from the Grampians, Vic.

Photographs: P.B. Bridgewater

33 "Symphomyrtus – Monocalyptus" forest with a diverse shrubland understorey, including *Banksia spinulosa*; New England National Park, N.S.W.

Photograph: G.R. Dyne



34 Mt Kosciusko from Charlotte Pass, N.S.W. In foreground is alpine herbfield with many species in flower. Note *Eucalyptus pauciflora* in mid-view.
Photograph: A.S. George



35 Alpine herbfield surrounding lake of glacial origin. The dominant flowering species is *Celmisia*. Blue Lake, Kosciusko National Park, N.S.W.
Photograph: A.D. Chapman



36 Wind-pruned *Eucalyptus pauciflora* from the Brindabella Range, A.C.T. Note extent of snowlie.
Photograph: R.C. Longmore



37 Temperate *Nothofagus cunninghamii* rainforest near Lake Pedder, Tas. Tree ferns (*Cyathea* sp.) are obvious in mid-view.

Photograph: A.S. George

38 *Gymnoschoenus sphaerocephalus* sedgeland from near Queenstown, Tas. This species forms extensive plains (termed Buttongrass plains) in western Tas.

Photograph: P.B. Bridgewater

39 Forester Kangaroo (*Macropus giganteus*) resting in "Symphomyrtus - Monocalyptus" forest, eastern Tas. The understorey is typical of such forests which have been extensively altered by human intervention.

Photograph: R.C. Longmore

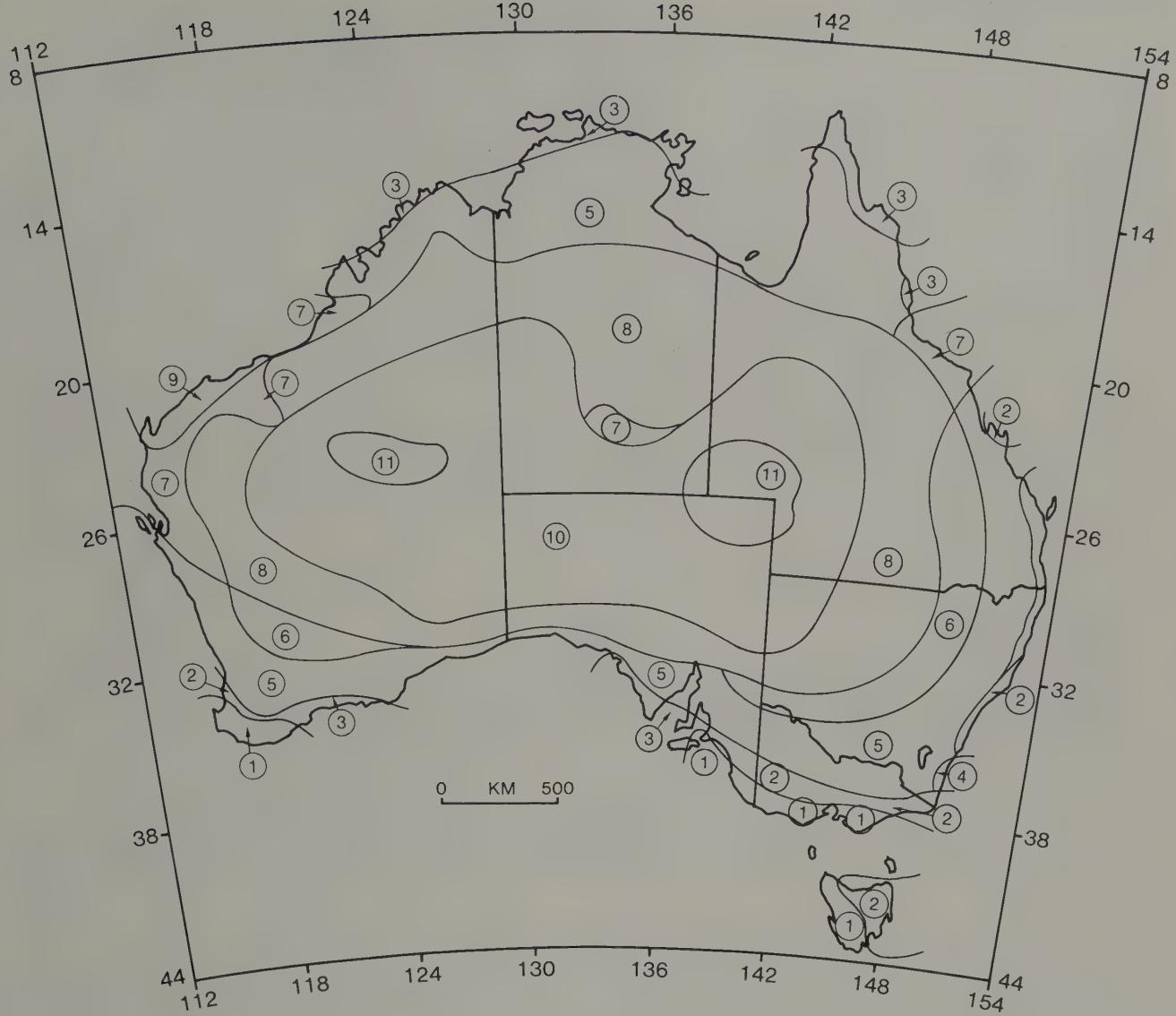


Figure 4.2 Climate variability in Australia. Low index numbers indicate a combined low range of annual temperature and little variability in the annual rainfall. High index numbers indicate both high range of annual temperature and great variability in annual rainfall.

also are recognized by Aborigines in the Arnhem Land region of the Northern Territory and the Dampierland Peninsula, Western Australia (Smith & Kalotas, 1985) and can be correlated with minor, but discernible, fluctuations in temperature and rainfall. In marked contrast, most European inhabitants of the region today recognize only two divisions of the year, the "wet" and the "dry".

Another way of viewing climate is through the climate types of Bagnouls & Gaussen, Walter and others, discussed by Gentilli (1972). Walter & Lieth (1967) document a number of distinct climate types for the world. Australia has four of these climate types, described below using the Roman numeral identification codes and descriptive terms of Walter & Lieth (1967).

II. Tropical type. Some seasonality in the mean daily temperature and with rainfall concentrated in the summer months (as Darwin, Cairns, Broome).

III. Subtropical dry type. Very low rainfall, high daytime temperature in summer with low winter minima (to zero) (as Port Hedland, Alice Springs, Port Augusta, Broken Hill).

IV. Transitional zone with winter rain. Very little summer rainfall, but receives cyclonic rains in winter. Typically no cold season, but permanent summer drought (as Perth, Esperance, Port Lincoln, Adelaide).

V. Warm temperate type. No noticeable winter, with year-round rainfall (as Melbourne, Sydney).

The northern New South Wales/southeastern Queensland region is a transition zone between the warm temperate/tropical types (II/V).

Figures 4.3 and 4.4 show examples of climate types and the points of change. At the 26th parallel of latitude there is a major change in climate type on both the eastern and western coasts. A major influence is the change from winter (or non-seasonal) rainfall in the south to summer (or cyclonic) rainfall in the north. There is a similar boundary running north/south from the Gulf of Carpentaria to the Southern Gulfs region of South Australia.

At the Southern Gulfs region in South Australia, the pronounced winter rainfall climate type gives way to the non-seasonal type. In the north, the year-round rainfall conditions of eastern Queensland give way to a predominantly wet/dry

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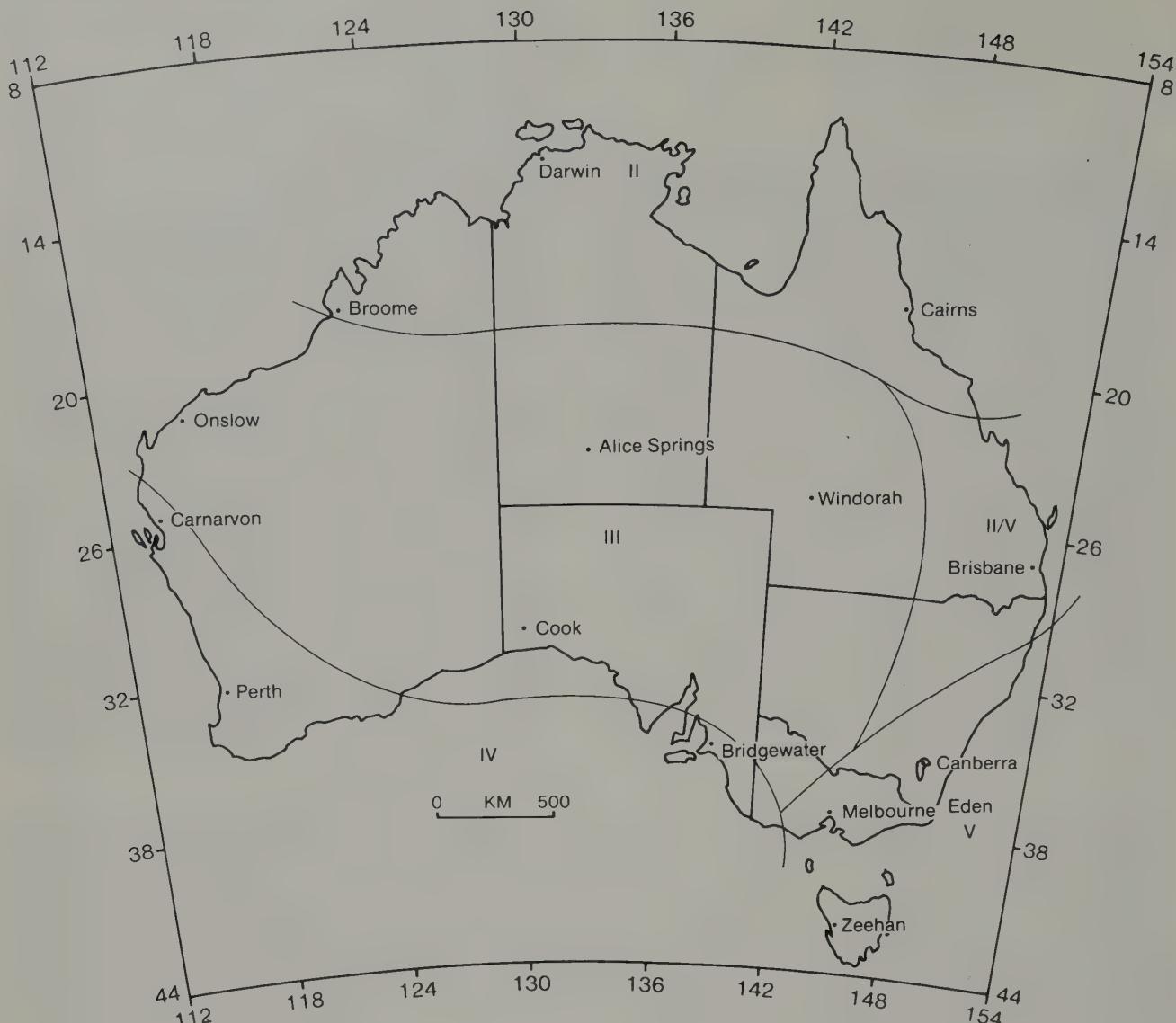


Figure 4.3 Distribution of climate types in Australia. The climate diagrams for localities in each area are shown in Fig. 4.4.

tropical system in the eastern part of the Gulf of Carpentaria. These wet/dry tropics become drier in a westward direction across the Northern Territory.

PHYSIOGRAPHY, GEOLOGY AND SOILS

Physiographically, Australia is a compact island continent. It is divided into very unequal parts by the Great Dividing Range, which is a watershed rather than a mountain range. The highest points of the Great Divide rarely exceed 1,500 to 1,800 m and the Great Divide is interrupted by a number of wide gaps among which are those near Newcastle, Rockhampton and Townsville. The highest parts of the Great Divide occur in the southeast and this, given the relatively high latitudes, has allowed the development of small areas of alpine environment. Mt Kosciusko, at 2,228 m, is the highest point in Australia.

West of the Great Dividing Range there are few mountains of significance. The major exceptions to this are the MacDonnell Ranges in Central Australia (>1,500 m), the Hamersley Ranges in northwestern Australia and the Stirling Range

in the southwest. Bluff Knoll at 1,073 m is the highest point in the Stirling Range and often carries snow for brief periods during winter. Mt Meharry (1,250 m) in the Hamersley Range is the highest point in Western Australia.

The major physiographic barriers to the distribution of biota in Australia are the Nullarbor Plain and Great Victorian Desert immediately north of the Great Australian Bight. These barriers effectively separate the well-watered regions of the southwest and southeast of the continent. The limestone Nullarbor Plain has been derived from a shallow Tertiary sea, which, during that era, provided an even more effective barrier. There is no similar barrier in central or northern Australia.

Geologically, the land surface of Australia is extremely old. While there have been comparatively minor morphological changes since the Tertiary with some glaciation in the Pleistocene, the surface of Australia reflects weathering processes on a landscape much of which has been stable and dry land for most of the last 400 million years (see Noakes, 1966).

Large areas of western and central Australia are covered by laterites which are the product of soils developed under the warm, wet conditions prevailing in the Tertiary. Other large

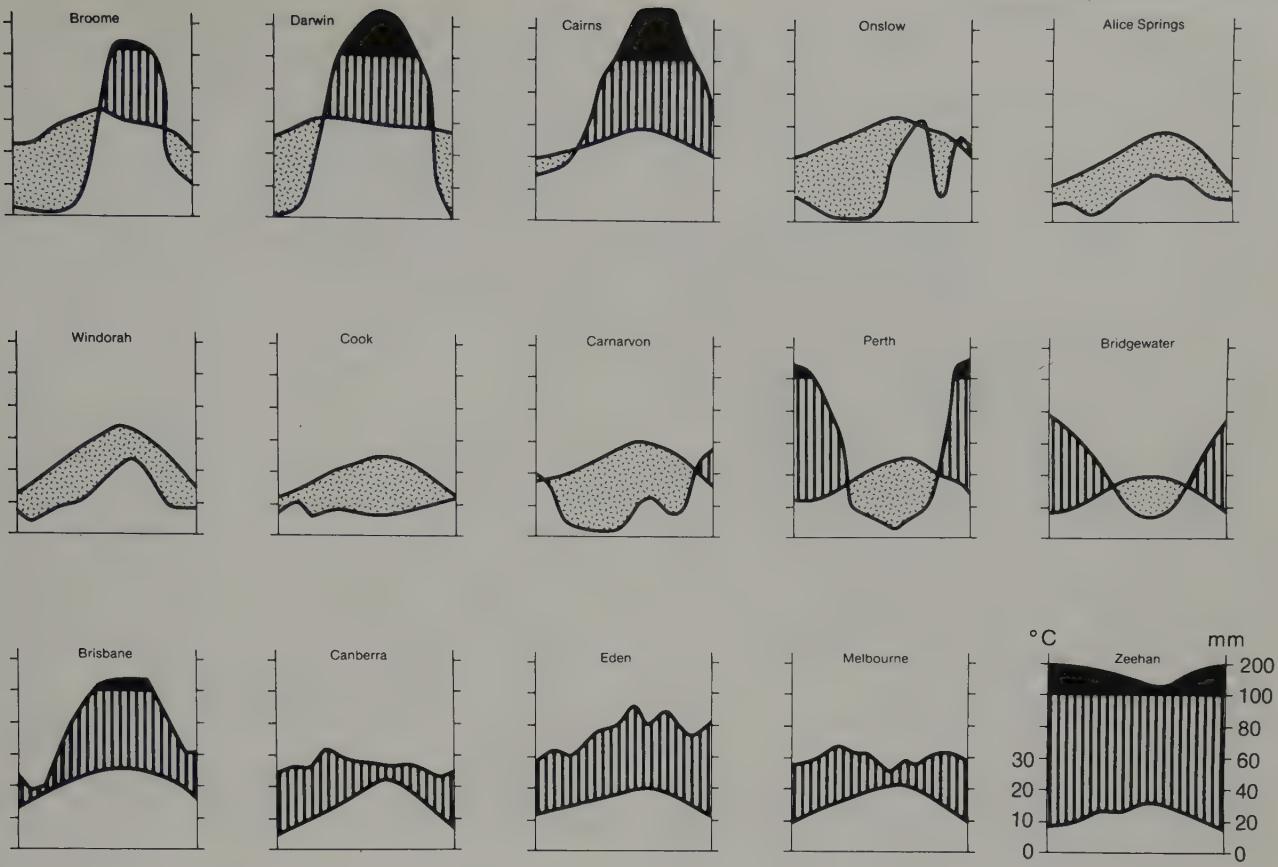


Figure 4.4 Examples of the major climate types in Australia (after Walter & Lieth 1967). Ordinate divisions = 10°C or 20 mm of rainfall. Where humid conditions prevail (rainfall curve above temperature curve) the diagram has longitudinal hatching. Dry conditions (rainfall curve below temperature curve) are indicated by stippling. Rainfall in excess of 100 mm is indicated by black shading, with the scale reduced by one-tenth. Geographical positions of the localities are given in Fig. 4.3.

areas of Australia have deposits of various sands, which in turn are the results of weathering on laterites, sandstones and granites. Erosion cycles of surface rock in most of Australia are at an advanced stage. Most surface soil geology systems are homogeneous. Although arid and semi-arid areas predominate in Australia, most carry considerable perennial vegetation. Deserts, defined as areas largely free of perennial vegetation, are rare in Australia and such as exist are chiefly of recent anthropogenous origin.

Large areas of arid Australia feature "break-away" structures, where the laterite caps of cliffs or mesas remain while the softer clays underneath are more rapidly eroded. Such "break-aways" often form the watershed for ephemeral water courses. Where such rivers and creeks drain to the sea (exorheic), the river beds are sandy or gravelly and the river edges support freshwater vegetation.

The southeastern region of the continent has relatively newer sediments than the rest of the continent and has suffered both the process of glaciation in relatively recent times and periods of volcanic activity since the Tertiary. Major structural elements of the continent are as discussed in Doutch (1979), to which the reader is referred for more detailed description.

Much of the interior of the continent, however, is characterized by internal (endorheic) or non-directional (arheic) drainage, with watercourses often forming chains of typically dry saline lakes. The prime example of endorheic systems are the rivers draining the channel country of southwestern Queensland into the Lake Eyre Basin. The basin has been filled on only three occasions since European settlement. Most of the semi-arid regions have arheic systems of drainage.

The ionic composition of inland water bodies in Australia is rather different from that of other parts of the world. Sodium and chloride tend to dominate both saline and fresh waters instead of calcium and bicarbonate (Bayly & Williams, 1973). This feature arises as a consequence of the "overriding importance of atmospheric supply of ocean salts to inland waters" (Bayly & Williams, 1973).

Australian soils are amongst the most nutrient poor in the world, largely as a result of their ancient derivation, allowing considerable leaching over the years. Detailed information on soils and their distribution may be found in Northcote *et al.* (1960–68) and Northcote *et al.* (1975).

Two main groupings of Australian soils are recognized, on the basis of their weathering. Where the soil parent material was subject to deep weathering during the Tertiary, the results are massive red and yellow earths, earthy loams, gravels and red siliceous sands. Where the material was weathered during the increasingly arid Quaternary period, the soils that result include calcareous earths, red and yellow duplex soils, saline and cracking clays, shallow soils and loams (including calcareous and saline loams). Soils in present day high rainfall areas are less alkaline than soils in present day arid areas (Northcote & Wright, 1982).

VEGETATION

Australian vegetation has been a subject of study since the start of the 20th Century, although generalized studies had resulted from the details brought back by the 19th Century explorers. Australian vegetation studies reflect an Anglo-

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American approach to description and documentation. Beadle & Costin (1952) present the first national attempt at vegetation classification. Specht (1970) produced a scheme for the description of Australian vegetation which, although modified (Specht, 1981), has remained largely unchanged. Walker (1984) offers a different perspective on the scheme of Specht (1981).

Many of the vegetation terms devised by Specht have been used with greater or lesser modification since 1970 in studies where vegetation description has been needed. Beadle (1981) produced a major treatise on Australian vegetation, using a refined form of the terminology of Beadle & Costin (1952), based on dominant species in association with a series of structural forms. This classification partly reflects Specht (1970), but it diverges from it by including more floristic detail and not emphasizing the height/density classes.

Detailed knowledge of Australian vegetation is still somewhat off, although the works of Beadle (1981) and Specht *et al.* (1974) have provided a basic framework. Despite the comment by Doing (1970) that "it is clear that floristic criteria should be applied for a coherent classification of vegetation", few studies in fact have employed such criteria. We are faced, thus, with problems of definition when referring to vegetation. This frustrates few people more deeply than zoologists, who argue the need for a handy form of vegetation description in order to relate faunal data with the wider environment.

Despite the size of Australia and apparent complexity of the vegetation pattern at a local level, vegetation expressed as landscape texture at the continental scale has great simplicity. Authors such as Beadle (1981) have recognized that there are a few key genera, each of which has many species dominating vegetation throughout Australia. These genera are *Eucalyptus*, *Melaleuca*, *Acacia*, *Triodia* and *Plectrachne*. The dominance of these genera assures a consistent physiognomic framework whether in tropical, temperate or arid Australia. Pryor & Johnson (1971) have discussed a number of subgenera within *Eucalyptus*. These subgenera have been used here to highlight a number of vegetation features impossible to describe from the generic standpoint of *Eucalyptus*, although the generic name is used where generality is helpful.

Previous small-scale vegetation maps of Australia have presented a mainly structural view of the vegetation (Williams, 1955; Carnahan, 1976). For this Chapter a vegetation map of Australia, based on the structural terminology of Anon (1973) and using limited floristic descriptors, has been specially prepared (see map in colour section). This map has been developed from those of Doing (1970), Carnahan (1976), Beadle (1981) and the author's own field experience. It is an attempt to produce a simplified, continental exposition of major vegetation patterns. As a small-scale synoptic map the boundaries should be viewed as indicative, rather than precise. Mapping units recognized are:

Tropical/Subtropical evergreen wooded vegetation

- 1 "Eudesmia" – "Corymbia" – "Blakella" – "Sympphyomyrtus" forest or woodland
- 2 "Corymbia" – "Blakella" – "Sympphyomyrtus" woodland
- 3 *Acacia* woodland
- 4 *Melaleuca* shrubland (Paperbark)
- 5 "Corymbia" – "Sympphyomyrtus" woodland
- 6 "Sympphyomyrtus" – "Monocalyptus" forest
- 7 *Angophora* – "Eudesmia" – "Corymbia" – "Blakella" – "Sympphyomyrtus" woodland
- 8 "Monocalyptus" – "Sympphyomyrtus" – "Idogines" forest
- 9 "Corymbia" – "Sympphyomyrtus" – "Gaugea" forest
- 10 Tropical rainforest
- 11 Subtropical rainforest
- 12 Tidal (mangrove) forest

Semi-arid grassland and shrublands

- 13 *Dichanthium* grassland (Blue Grass)
- 14 *Astrebla* grassland (Mitchell Grass)
- 15 *Zygochloa* grassland (Cane Grass)
- 16 *Triodia* grassland (Spinifex), with an open tree layer of *Acacia*, *Allocasuarina* or *Eucalyptus*
- 17 *Atriplex* – *Maireana* semi-succulent shrubland (Saltbush)
- 18 "Eudesmia" – "Monocalyptus" – "Sympphyomyrtus" sclerophyllous shrubland (Mallee)
- 19 *Acacia* shrubland (Mulga)
- 20 *Acacia* thicket, with *Triodia* understorey

Temperate forests, grasslands and shrubland

- 21 "Corymbia" – "Monocalyptus" – "Sympphyomyrtus" forest
- 22 "Sympphyomyrtus" woodland, with scattered shrubs understorey
- 23 "Sympphyomyrtus" woodland, with shrub or grass understorey
- 24 "Sympphyomyrtus" woodland, with *Bothriochloa* / *Heteropogon* understorey
- 25 *Stipa* grassland
- 26 "Monocalyptus" woodland
- 27 Alpine sclerophyllous shrubland
- 28 "Sympphyomyrtus" – "Monocalyptus" forest
- 29 "Corymbia" – "Sympphyomyrtus" – "Monocalyptus" winter-rain forest
- 30 "Sympphyomyrtus" winter-rain sclerophyllous forest
- 31 *Banksia* – "Corymbia" – "Monocalyptus" woodland
- 32 Proteaceae – Myrtaceae – Mimosaceae – Epacridaceae shrubland
- 33 *Nothofagus* rainforest
- 34 *Gymnoschoenus* sedgeland

Variation in these vegetation types is either east-west (as in types 1, 18) or north-south (as in 21, 23, 32) or both (as in 16). Nomenclature of these vegetation types is generalized and may not cover all expressions of the type. For example, type 18 only has "Eudesmia" species in Western Australia, although the name is used across the continent.

Obviously, within the broad parameters of these vegetation types, there is considerable local variation. At a local level, vegetation needs to have appropriate floristic descriptors – the mainly structural descriptions of the vegetation presented above are rarely sufficient to allow for comparisons with other areas or to form an effective means for documenting the interaction between fauna and vegetation. Some limited detail, including localized vegetation types not mapped, is given in the Regional Landscapes Section later in this Chapter.

Williams (1982) notes the complexity that can be observed within generalized vegetation formations by citing work of Boyland (1974) and Perry & Lazarides (1962). Williams uses Boyland's definition of up to 11 associations with an *Acacia aneura* predominant association in southwest Queensland as evidence of complexity and patchiness in vegetation pattern. More importantly, Williams draws attention to the complexity uncovered by Perry & Lazarides (1962) when they analysed the shrub and ground stratum of some arid zone communities separately and then recombined them. Although their work was focused on the arid zone, it is just as valid for all vegetation.

Separate analyses of vegetation strata can yield new insights into the vegetation-environment relationship as shown in Bridgewater (1982). On the eastern coast of Australia the apparently continuously varying forests of the Great Diving Range show pronounced boundaries when viewed from the perspective of the lower stratum, although the tree species produce an apparent continuum (Ashton, 1976).

The enormous species richness documented for a number of areas of Australia (southwest, southeast coast, wallum area of Queensland) has often confused authors attempting floristic description of vegetation communities. Much of this species richness can be attributed to species occupying niches that are of the regeneration type (Grubb, 1977). Plant communities which determine vegetation pattern in Australia, as in the rest of the world, are characterized by rather few species, but with varying contributions from numerous species which add to the diversity of the community. The contribution of those species to the maintenance and prolongation of the communities remains an intriguing question.

FIRE

"As an ecological factor in arid Australia, fire is as ubiquitous as drought" (Main, 1976). The role of fire in all Australian ecosystems is receiving increasing attention, particularly in view of the potential use of fire as a management tool. Excellent reviews in recent years have contributed to the development of fire science, see Gill *et al.* (1981). For a number of sclerophyll communities in southern Australia, fire is known to be important both for nutrient recycling and for seed release and germination of many species. Holocaust wildfires in the normally wet "Symphyomyrtus" forests of southwestern and southeastern Australia are essential for the germination of such major tree species as *Eucalyptus diversicolor* and *E. regnans*. What has also become clear is the extent to which many faunal species respond to fire by colonizing particular stages in the regeneration of communities (Christensen *et al.*, 1981).

The term "fire (or pyrrhic) succession" has been used for many years in ecological literature. Succession conveys the impression that there is a linear sequence of communities, whereas what we see is community regeneration through a series of stages. The precise sequence of regeneration stages depends on the other environmental disturbances operating in the burnt area (Noble & Slatyer, 1981).

Many Australian plant species regenerate from below-ground stems or lignotubers while others can regenerate only from seed. Particular examples of seed regenerators are the native gymnosperms (*e.g.*, *Callitris*), species with serotinous cones (*e.g.* some *Banksia* species) and some eucalypts (*e.g.*, *Eucalyptus diversicolor*, *E. regnans*).

While the numbers of particular plant species may vary in the regeneration sequence following fire and may vary with the time and intensity of the fire (Cockburn, 1978), frequently all species of the plant community are present at all stages of the community regeneration. Some faunal species use exclusively a community in a particular regeneration stage, *e.g.* Fox & Fox (1978). Others may simply use a regeneration stage en passant between other stages. Faunal species richness, therefore, depends on a matrix of regeneration stages for food, shelter and breeding purposes.

Fire is a major factor in creating and maintaining the landscape texture (patchiness). Fire has also been responsible for creating major shifts in vegetation pattern (see Noble & Slatyer, 1981). Particular examples include the *Gymnoschoenus* sedgeland, *Nothofagus* temperate rainforest and "Symphyomyrtus" sclerophyllous forest landscape in western Tasmania. Jackson (1968) describes these changes in regenerating vegetation in similar terms to the genetic drift concept used by population geneticists. The term "ecological drift" was born and neatly describes the flux between these three vegetation types. Fire frequency determines the waxing and waning of the three types, with low fire frequencies favouring *Nothofagus*, while high frequencies (12 to 25 years) favour the *Gymnoschoenus* sedgeland.

Even intense wildfires produce a patchy landscape — small, relatively unaffected islands act as seed areas for regeneration (Christensen & Kimber, 1975). Fires in arid areas may have a variety of effects, depending on the time of year of burning. Summer fires (a natural occurrence in *Triodia* grasslands) control shrub invasions (Suijdendorp, 1981). Survival and regeneration of the grasses depend on the amount and timing of the next rains. Winter firing in *Triodia pungens-Acacia translucens* along the Pilbara coast of northwestern Australia effectively promotes the increasing dominance of *Acacia*, particularly if aided by sheep grazing following the fire.

A major complicating factor affecting fire in Australian environments is human activity. Australian Aboriginals used fire as a tool for environmental manipulation. Major changes brought on by activities following European colonization since 1788 have been: species extinctions, changes in ecosystem structure and function, wider distribution of exotic plants and animals and creation of new synthetic communities (Bridgewater & Backshall, 1981). These effects are visible in all continents, but are pronounced particularly in Australia and other recently colonized areas *e.g.* western North America, western South America. Fauna and flora suffered severe disruption in these areas with the discovery and settlement by Europeans from the late 18th Century to the present.

That is not to say the landscapes of Australia were unaffected by people prior to settlement by Europeans. There is increasing evidence that for a period of at least 40,000 years Aborigines used fire as the most important tool in modifying their environment by what is best described as "natural engineering", *e.g.* Nicholson (1981), Haynes (1985).

REGIONAL LANDSCAPES OF AUSTRALIA

The landscape regions described in this Section are those of Barlow (1985) and are the geographic regions used for description of distribution in all publications of the Australian Biological Resources Study. Climatic and vegetation terminology is that used in the relevant sections earlier in this Chapter. Figure 4.5 illustrates these regions. For each region brief details of climate, physiography, geology and vegetation are given. Detail presented here is not meant to be exhaustive, but indicative of key or interacting features. Relevant State Government Departments are likely to be the best source of further information on these regions.

1. Kimberley.

Climate: Tropical type (II).

Physiography and Geology: To the south, the region is drained by the Fitzroy River, which empties into King Sound, while the Ord and Durack Rivers drain north into Cambridge Gulf. The central northern region is drained by the Drysdale River which emerges at the sea just west of Cape Londonderry.

Landforms of the region range from the red sandy plains of the southwest to the hills and mountains of northern Kimberley and the limestone gorges of the Fitzroy Plain. These limestones are the remnants of a coastal barrier reef from the Devonian period.

The dominant rock formation is sandstone, often forming steep scarps. The sedimentary rocks have basalt intrusions of various ages. Some of the older basalts carry lateritic surfaces developed mainly during the Tertiary. Some laterites contain bauxite.

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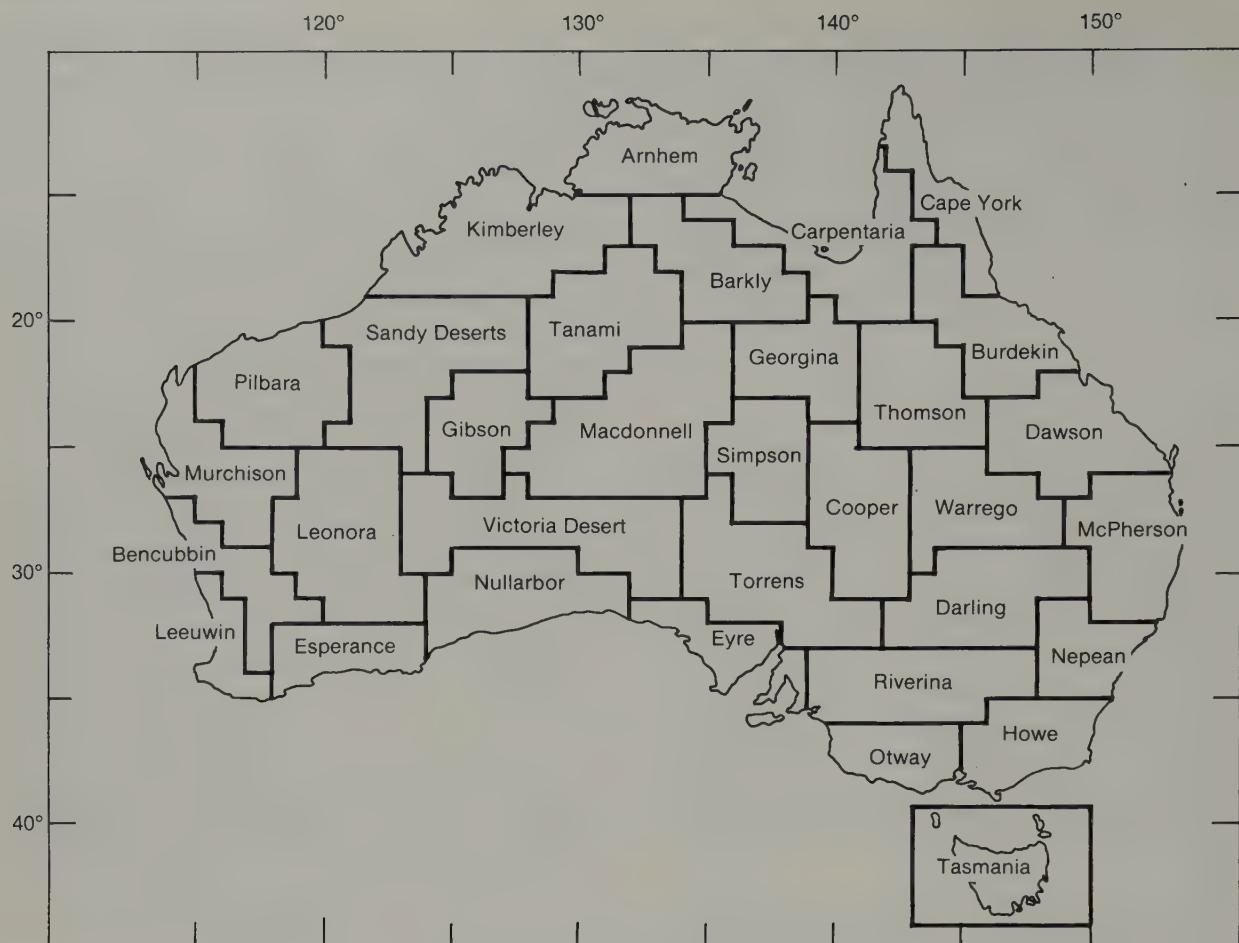


Figure 4.5 Map showing natural regions of Australia described in text. (After Barlow, 1985)

Vegetation: The coastal parts of the region carry "Eudesmia" – "Corymbia" – "Blakella" – "Sympphyomyrtus" forest, grading inland to woodland. Around the coastal region of Broome and Derby, local dominance by the deciduous *Adansonia gregorii* (Baobab) occurs. In higher rainfall sites a "dry rain-forest" vegetation type (termed vine thicket) occurs.

Towards the southern edge, grasslands of *Astrebla* (chiefly on soils derived from the limestones) and *Triodia* occur. On the red sand area an *Acacia* dominated community with a grass understorey, termed Pindan, occurs (Beard, 1978). Extensive mangrove and saltflat vegetation occur in the major estuaries.

2. Arnhem.

Climate: Tropical type (II) – typically wetter and cooler than Kimberley.

Physiography and Geology: Comprising the drainage systems of Daly, Alligator and Roper Rivers, the region has a physiography of plateaus dissected by deep, straight valleys. Black soil plains dominate the land near the coast. In the wet season, numerous swamps and streams, turning to billabongs as the dry season approaches, feature prominently on these plains. Termite mounds are a common feature of the landscape.

While the main rocks are Precambrian sandstones, with some granite intrusions, the wide coastal plains consist of fine clays from the weathering of mudstones. Laterite ridges are frequent on these plains, often featuring at the coast as low

cliffs or bluffs. Large areas of mudflat and tidal swamp (including extensive mangrove forest) occur around the coast and line the wide inlets.

Vegetation: "Eudesmia" – "Corymbia" – "Blakella" – "Sympphyomyrtus" forest grading to woodland in the interior, forms the major vegetation of the region. In coastal regions the black soil plains support grassland, with well-developed mangrove forest in sheltered embayments and estuaries of the western and northern coasts. Extensive stands of the soft-wood *Callitris intratropica* occur on sandy and gravelly soils. These soils also support genera of the families Proteaceae and Myrtaceae, typically associated with more temperate regions (e.g., *Banksia*, *Calytrix*). Wetter sheltered sites carry forms of rainforest.

Modification of the plains and wetlands has occurred due to the introduction of feral domestic animals (Water Buffalo, Donkey) in both Arnhem and Kimberley regions.

3. Barkly.

Climate: Transitional between Tropical (II) and Subtropical dry type (III).

Physiography and Geology: The bulk of this region lies in a low depression, with plains to the northeast and southwest. While most of the region has no external drainage, there are a number of rivers draining the edge of the tableland and coastal ranges to the Gulf of Carpentaria.

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The flat plains are underlain by limestone, giving way to sandstones in the north. Weathering of these limestones has produced a cover of thick clays, interspersed with occasional low gravelly lateritic rises.

Vegetation: Because of the calcareous clay soils which dominate this region, the major vegetation is *Astrebla* grassland, with occasional trees (*Eucalyptus coolabah*) in the depressions and ephemeral water courses. Woodlands dominated by *Acacia shirleyi* assume occasional importance in this landscape.

4. Carpentaria.

Climate: Tropical type (II).

Physiography and Geology: This region includes the seasonally-inundated lowlands around the southern part of the Gulf of Carpentaria. Many rivers, almost all seasonal, emerge from the limestone plains of the Barkly Tableland to the south and the ranges of Cape York Peninsula to the east. Between the land and sea is a band of barren mudflats, which can stretch inland for up to 30 km.

The lowlands carry mainly deep clays interspersed by sandy ridges and fragments of an ancient lateritic surface. The area at the base of Cape York Peninsula exemplifies the results of past river action on sandstones, having sand deposits up to 10 to 15 m deep.

Vegetation: *Dichanthium* or *Astrebla* grassland occurs on the clay plains while *Melaleuca* shrublands dominate the sandy soils. These shrublands also have species of Proteaceae, Myrtaceae and Fabaceae as major components. *Acacia* and "Corymbia" - "Blakella" - "Sympphyomyrtus" woodlands dominate the ranges. Some sites also carry "rainforest scrub", with components of tree and shrub species from the Indo-Malayan floristic element. Species-poor mangrove forest occurs at the high tide level.

5. Pilbara.

Climate: Subtropical dry type (III).

Physiography and Geology: With uplands and associated drainage systems of the Ashburton, Fortescue and DeGrey Rivers, this region has the highest mountains in the western part of the continent (Hammersley Range) with Mt MeHarry (1,250 m) the highest point. To the east the ranges grade into low ridges, surrounded increasingly by sandy plains. The hills are incised by deep gorges, often carrying permanent water holes. To the northwest, gently rolling hills end in a flat coastal plain of varying width.

A complex of sedimentary and intrusive rocks, with greenstones, sandstones and metamorphic rocks interspersed by granitic intrusions, forms the major elevated features. Weathering of the laterized surfaces produces "break-away" landscapes of flat-topped, broken-edged hills above a level plain criss-crossed by the anastomosing branches of feeder creeks to the major rivers. Sandstone and banded ironstone sedimentary rocks form the major peaks of the Hammersley Range.

Vegetation: A complex vegetation pattern of *Triodia* grassland, *Acacia aneura* woodland on the flood plains and *Triodia* grassland with open tree layer of *Eucalyptus leucophloia* on the stony hills is typical of this region. Fringing forests of the river and creek-lines are dominated by *E. camaldulensis* and *E. coolabah*.

Despite a very low, uncertain rainfall and nutrient-poor soils, the landscape texture is varied and there is a high species richness of both perennial shrubs and ephemeral grasses and forbs.

6. Sandy Deserts.

Climate: Subtropical dry type (III).

Physiography and Geology: Ten to 30 m high sand dunes up to 300 km long trend westerly, turning northwesterly closer to the coast. Occasional salinas or playas are found. Sedimentary sandstones have weathered to provide the sand for the deserts and are now largely buried by the dune fields.

Vegetation: *Triodia* grasslands form the main vegetation cover for the inland portion of this region. Towards the coast, dominance by *Acacia* species increases. At the coast, the white sands of the 80 Mile Beach merge with the red dune ridges of the central "desert" regions.

7. Gibson.

Climate: Subtropical dry type (III).

Physiography and Geology: Dune fields, residual uplands and lateritic plains form the Gibson Desert, with lateritic plains being the dominant landform.

Sand-dunes, rocky rises and ridges protruding through the sand dominate much of this region, culminating in the Warburton Ridge which divides the Gibson Desert from the Great Victoria Desert (see Region 12).

Vegetation: *Triodia* grassland is the major vegetation, with open tree layer of *Eucalyptus* and/or *Acacia* on the ridges, ranges, drainage lines for ephemeral waterflow and depressions.

8. Tanami.

Climate: Subtropical dry type (III).

Physiography and Geology: This is a region of plains and widely-spaced dune systems, trending northwesterly.

Apart from the weathered sandstones buried by dune fields, a small granitic intrusion occurs, now weathered into a series of tors.

Vegetation: *Triodia* grassland dominates with depressions carrying an open tree layer of *Allocasuarina decaisneana*.

9. MacDonnell.

Climate: Subtropical dry type (III).

Physiography and Geology: The region consists of the high plains (>500 m altitude) surrounding the uplands of the MacDonnell and Musgrave Ranges. Large salinas and numerous dry-bed river systems abound, all draining into the surrounding regions. Lake Amadeus and Lake Neale, largest of the salinas divide the region. Apart from the range systems there are three "Great Tors" of the Olgas, Mt Connor and Ayers Rock. The origin of these structures is believed to date from the Precambrian glaciation when Australia lay much further south.

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Granites and sedimentary rocks (including limestones and quartzites) form the MacDonnell Ranges, while the Musgrave Range has both sedimentary and glacial deposits contemporaneous with similar rocks in the Flinders Ranges (see Region 25). The "Great Tors" are all formed from glacial deposits – the Olgas are uplifted masses of poorly-sorted conglomerates, while Ayers Rock and Mt Conner are formed from much water-borne finely sorted material of glacial origin which was subsequently uplifted.

Vegetation: The complex of ranges, plains and low rocky eminences results in a similarly complex vegetation pattern. Major vegetation types are *Triodia* grassland; *Acacia* woodland; *Allocasuarina decaisneana* groves; woodland dominated by various *Eucalyptus* species on the ranges and plains; *Atriplex* – *Maireana* semi-succulent shrubland. Of interest also is the persistence of a palm and cycad species (*Livistona mariae* and *Macrozamia macdonnellii*) in a deep gorge of the Macdonnell Ranges, suggesting the vegetation of earlier, wetter climates.

10. Murchison.

Climate: This region marks the boundary between Subtropical dry type (III) and the Transitional zone with winter rainfall (IV).

Physiography and Geology: The easterly part of this region comprises the Yilgarn Shield – the ancient and geologically complex block of archaean rocks. Along the western edge, younger (Tertiary) rocks are overlain by sandy deposits forming a wide lowland, drowned by Shark Bay in the south, Exmouth Gulf in the north, with the usually dry Lake Macleod in between. In the northwest of this region lies a low range of hills, termed the Cape Range, along the western side of Exmouth Gulf. These low hills are formed from sandstones and limestones and are cut by steep-sided gorges.

Vegetation: *Acacia*, particularly *A. aneura*, woodland is the major vegetation of this region with "Symphyomyrtus" woodland on the low hills and ranges. In the south of the region, representation of plant species from the South Western Province (Beard, 1980) increases.

11. Leonora.

Climate: Subtropical dry type (III).

Physiography and Geology: Jutson, a pioneer writer on the physiography of Western Australia, suggested the name "Salinaland" for this region, a name which emphasized the dominant feature of salt lakes in the landscape. These chains of lakes may represent the shrunken remains of ancient rivers from a wetter climatic era. Such rivers may have drained this region both to the southwest and southeast.

Prolonged weathering of the underlying rocks, in a former humid climate, led to the formation of extensive bands of laterites, with a hard resistant "duricrust". Uplifting of this landscape in the Tertiary allowed erosion to take place, providing the typical "break-away" features. Occasional resistant masses remain dominant features in this otherwise subdued landscape. To the east, the ancient rocks are covered by the sand of the Great Victoria Desert.

Vegetation: Much of the region is covered by *Acacia aneura* woodland with *Eragrostis* spp. in the understorey, but this is replaced in the south by "Symphyomyrtus" woodland over an understorey of shrub species (rather than grasses). In the

extreme southeast, the major vegetation is "Eudesmia" – "Monocalyptus" – "Symphyomyrtus" sclerophyllous shrubland.

12. Victoria Desert.

Climate: Subtropical dry type (III).

Physiography and Geology: Mainly long, regular, westward trending sand ridges form the landscape of this region. Occasional salinas, indicating previous drainage systems, occur south from the Musgrave Range. A sharp boundary between the Nullarbor to the south (see Region 13) and the Great Victoria Desert is formed by stabilized sandridges 10 to 50 m high. Dune fields diverge at the eastern end, with a southerly group trending to the Eyre Peninsula and a group trending northerly to the Simpson Desert (see Region 22).

Vegetation: Although *Triodia* grassland is common, this region has better developed woodlands and shrubland than Regions 6, 7 and 8. *Allocasuarina*, *Acacia*, *Callitris* and *Eucalyptus* species form dense thickets, particularly in depressions where groundwater is close to the surface. *Eucalyptus gongylocarpa* thickets are a prominent feature of this landscape region.

13. Nullarbor.

Climate: An arid form of the Transitional zone with winter rainfall (IV), with a narrow coastal strip receiving significantly greater rainfall than the inland plain.

Physiology and Geology: The Nullarbor has a very simple geological structure - being a flat elevated limestone plain, with underlying horizontal sediments, which tend to reduce erosion. This plain, for the most part, ends in spectacular vertical cliffs (some 90 m high) along the Great Australian Bight. At the eastern and western edges of the region a narrow sandy plain acts as a buffer between the sea and the edge of the tableland. Drainage patterns on the plain tend to be shallow, with occasional depressions (termed dongas), supporting a few shrubs of *Myoporum* or *Acacia* species. Being permeable to water, and water soluble, this limestone plain has developed Australia's most elaborate cave system – often important faunal habitats.

Vegetation: Much of the region is characterized by *Atriplex* – *Maireana* semi-succulent shrubland, with "Eudesmia" – "Monocalyptus" – "Symphyomyrtus" sclerophyllous shrubland along the coastal fringe.

14. Bencubbin.

Climate: Transitional zone with winter rainfall (IV).

Physiology and Geology: Pronounced weathering of the ancient laterized surfaces has resulted in the development of extensive sand plains with projecting granitic zones and resistant lateritic break-aways. Chains of salinas occur in the east of the region, with stronger flowing rivers draining to the coast in the west.

Vegetation: Despite the poor soils of this region, landscape texture is very varied, with "Symphyomyrtus" woodland typical of the heavier soils and multi-species shrublands typical of the sandy soils and rocky outcrops. This region has been cleared extensively for wheat and sheep farming. Original

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vegetation remains only as isolated remnants. Species richness is very high and the landscape pattern has great variety. (e.g. Region 16).

15. Leeuwin.

Climate: Transitional zone with winter rainfall (IV).

Physiography and Geology: During the Tertiary this region shared with adjacent and inland regions the processes of weathering and surface rotting of igneous rocks to produce laterites. These laterized soils were then uplifted. A major difference, however, is the continuing wetter coastal climate of the Darling Escarpment which forms the western edge of the ancient shield. To the west, the edge of the plateau has produced sediments which fill a rift valley. These sediments now form a coastal plain with deposits of fluvial origin to the east, succeeded by three bands of aeolian sand dunes, of decreasing age to the west. Granitic intrusions occur throughout the shield edge, often forming the highest points on the western edge.

Vegetation: "Corymbia" – "Sympyomyrtus" – "Monocalyptus" winter-rain forest is the major vegetation, being replaced by "Sympyomyrtus" winter-rain sclerophyllous forest in the wetter southern areas. Coastal fringes and exposed sandy patches in the plateau region carry species-rich shrubland and *Banksia* – "Corymbia" – "Monocalyptus" woodland.

16. Esperance.

Climate: Transitional zone with winter rainfall (IV).

Physiography and Geology: Physiographically this region is composed of the edge of the laterized ancient plateau, with sandy plains forming a coastal fringe. In addition, there are several coastal ranges of more recent quartzites, shales and slates. The best known of these is the Stirling Range. Just south of this range is a granitic extrusion (the Porongorup Range) which attracts significantly greater rainfall than the average for this region and carries the most eastward forest vegetation dominated by *Eucalyptus diversicolor* (Karri).

Vegetation: Landscape texture is very varied and species richness is very high in this region. Most vegetation of the region is multi-species shrubland, extending inland to "Eudesmia" – "Monocalyptus" – "Sympyomyrtus" sclerophyllous shrubland. This vegetation exhibits considerable patchiness due to varying topographic and soil structures across the region.

17. Cape York.

Climate: Tropical type (II). Some localities may fall into the equatorial (I) category of Walter & Lieth (1967), but most such sites tend to have cooler winters than typical equatorial localities. Among the tropical sites in Australia the rainfall is heaviest and most persistent through the year in this region.

Physiography and Geology: Granite and sandstone rocks form the northern-most part of the Great Dividing Range, which ends as a granitic dome at Cape York. On the west, there are laterized surfaces that have been little eroded and are exposed as red cliffs on the west coast. Weathering of sandstone produces the sand plains which carry shrubland. During the dry season these shrublands are dry and arid, turning to "wet deserts" in the wet season. Tablelands west of

Cairns have been produced from Tertiary basalt flows, which have weathered to richer soils and carry extensive stands of rainforest.

Vegetation: Much of the region is covered by "Corymbia" – "Blakella" – "Sympyomyrtus" woodland, with some wetter areas covered by *Melaleuca* shrubland. Extensive areas of rainforest occur, especially on the richer soils and in areas of higher rainfall. These forests are species-rich with the dominants varying from site to site. Australia's most species-rich mangrove forests occur in this region, with extensive tidal forests extending upriver of all major estuaries.

18. Burdekin.

Climate: Tropical type (II).

Physiography and Geology: Major features of this region are the low ranges of the Great Divide, situated up to 300 km inland, and the higher ranges which occur closer to the coast. Geologically, it is complex with sediments interspersed by granitic intrusions and basaltic flows. The Burdekin River, after which the region is named, is the largest river draining to the Pacific Ocean.

In the southern part, the region has a gently undulating surface of weathered sedimentary rocks. In the western part of the region drainage is largely internal to the region.

Vegetation: "Corymbia" – "Sympyomyrtus" woodland covers the ranges and lowlands, with tropical rainforest on the ranges receiving greatest rainfall. To the inland, extensive clay patches carry *Acacia* woodland and small patches of *Astrebla* grassland.

19. Dawson.

Climate: Tropical type (II).

Physiography and Geology: The dominant features of the landscape in this region are alternating ranges and basins. Inland ranges have a greater elevation than the scattered central ranges. Granites, sandstones and basalts are the major rock types of the ranges. The basins are formed from large deposits of clays.

Drainage of the region is to the Pacific Ocean, via the Fitzroy and Dawson Rivers.

Vegetation: Complexity of landform is reflected in variety of landscape texture. The "Corymbia" – "Sympyomyrtus" woodland is characterised by *Eucalyptus crebra* woodland on the ranges and *E. populnea* and *Acacia harpophylla* woodland on the clay plains. Sandridges and lighter soils carry *Allocasuarina* woodland. Localized rainforest patches occur in sites which have nutrient rich soils and/or higher effective rainfall. Effective rainfall is the amount of rainfall actually received. In low-lying areas may be much more than the actual rainfall, due to run-off water accumulating from the surrounding hills.

20. Georgina.

Climate: Tropical type (II) transitional to Subtropical dry type (III).

Physiography and Geography: The region is one of plains, with the Isa Highlands forming a major relief feature. These highlands are sedimentary rocks intensely folded and with

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granite intrusions. The softer rocks (shales) have been eroded, leaving the ranges and ridges of harder rocks. Drainage is mostly arheic.

Vegetation: The ranges carry *Triodia* grassland, with an open tree layer of *Acacia* or *Eucalyptus*, or "Corymbia" – "Blakella" – "Symphyomyrtus" woodland dominated by eucalypts mixed with *Grevillea striata* and *Atalaya hemiglaucia*. *Astrebla* grassland covers the surrounding plains, giving way to *Triodia* grassland on poorer or sandy soils.

21. Thompson.

Climate: Subtropical dry type (III) transitional to Tropical type (II).

Physiography and Geology: Sandstone ridges form the eastern boundary of this area, while basaltic flows occur in the northeast. Lateritic plateaus, formed by the erosion-resistant duricrust are common in the northwest. To the south extensive clay plains, derived from the weathering of shales, form impermeable soils. These crack in the dry season, allowing surface material to fall into the crack, which then closes in the wet. This process is one of "self-mulching".

Aquifers are important in this region. Rainwater percolates through the sandstone ranges and is then forced out when it encounters impermeable shales. This gives rise to the phenomenon of "mound springs", which are the source of some rivers. These mound springs are also sites for many endemic invertebrates and even small fish. The presence of calcium carbonate in the waters has ensured the growth of tuffa or travertine – hence "mound" spring (see also Region 25).

Vegetation: Much of this region is covered by *Astrebla* grassland, with *Acacia* woodland occurring on deep clays. The lateritic ridges have a cover of *Triodia* grassland with scattered *Eucalyptus*, *Acacia* and *Grevillea* spp. To the north the basalt flows carry "Corymbia" – "Blakella" – "Symphyomyrtus" woodland with a *Themeda/Heteropogon* grass understorey.

22. Simpson.

Climate: Subtropical dry type (III). The climate of this region is the most arid of all Australian climates.

Physiography and Geology: As with Regions 6, 7, 8 and 12, the physiography is elongated dune systems in this case, trending north-northwest. Towards the edges of the region fragments of the lateritic rock plateaus are still preserved, protected from erosion by the hardened duricrust "cap". Clay swales lie between dunes.

Vegetation: The lower slopes of dunes are stabilized by species of *Triodia*. *Zygochloa paradoxa* forms an open grassland on the dune crests and upper slopes.

23. Cooper.

Climate: Subtropical dry type (III), transitional to Tropical type (II) in the east.

Physiography and Geology: This region frequently is referred to as the "Channel Country", from the mass of anastomosing watercourses which originate in the ranges of Thompson Region (21) and dissipate either into sand or, eventually, Lake Eyre and/or Lake Frome. Scattered through this region

are low, flat-topped hills and break-aways topped with laterite or silcrete. The river courses are gouged through alluvial plains or the disintegrated stony lateritic plains known as "gibber deserts".

Vegetation: *Triodia* and *Astrebla* grasslands form the major vegetation of these plains. The presence of *Atriplex* and other saltbush shrubland increases in the southern part of the region as does the cover *Acacia aneura* over the grass understorey.

24. Warrego.

Climate: Subtropical dry type (III) transitional to Tropical type (II).

Physiology and Geology: The headwaters of the Darling River lie in this region, which is mainly flat, save for sandstone ridges in the east and lateritic capped mesas scattered through the area.

Vegetation: As the climate is transitional, so the landscape texture appears quite complex. Open plains carry *Astrebla* grassland, with *Callitris* woodland on sandy soils and *Acacia harpophylla* or *Allocasuarina lepidophloia* woodland on clay soils. Lighter clay soils carry "Symphyomyrtus" woodland. In the western region *Acacia aneura* woodland is the major vegetation type.

25. Torrens.

Climate: Subtropical dry type (III).

Physiography and Geology: Salinas are a major feature of this region. A virtual semicircle of salt lakes surrounds the northern end of the Flinders Ranges. Much of the region is covered by weathered silcrete, forming the stony or gibber desert lands.

In the southeast, the Flinders Ranges consist of Precambrian sediments and granitic intrusions. The sedimentary material includes conglomerates, quartzites and limestones. "Mound springs" also are found in this region (see Region 21).

Vegetation: The Flinders Ranges carry "Symphyomyrtus" and *Callitris* woodlands while the plains are dominated by *Acacia* woodland and *Atriplex* – *Maireana* semi-succulent shrubland. The extensive salinas have *Halosarcia* dominated flats and marshes around their edges.

26. Darling.

Climate: Subtropical dry type (III) with increasing winter rainfall to the south of the region.

Physiography and Geology: Much of the region is a level lowland with the flood plains of the Darling River and its tributaries. To the east the ranges increase in height and structure while to the west there are few ranges. The main exception is the Mootwingee Range, a northeastward extension of the Barrier Range. The plains have extensive alluvial deposits of light brown soils, with crusts of ironstones and calcareous layers.

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Vegetation: Dense fringing forests of *Eucalyptus camaldulensis* line the major rivers, while *Acacia* and "Symphyomyrtus" woodlands are common on the plains. A frequent co-dominant with *Acacia* spp. is the Wilga (*Geijera parviflora*). The ranges carry *Callitris* and "Symphyomyrtus" woodlands.

27. Eyre.

Climate: Transitional with winter rainfall (IV) to Subtropical dry type (III) on the inland margins.

Physiography and Geology: The Eyre Peninsula, Yorke Peninsula, Mount Lofty Ranges, Fleurieu Peninsula and Kangaroo Island constitute this region. Although fragmented, these areas share a common structural history. The Eyre Peninsula is covered largely by aeolian sands over ancient crystalline and sedimentary rocks. Extensive recent calcrete deposits are also a feature of the peninsula.

Relatively recent (late Tertiary) earth movements raised the Mount Lofty Ranges, which extend south to the subdued remnant of Kangaroo Island and north to the Flinders Ranges. Fringes of lowland along the edge of the Gulfs extend to Yorke Peninsula.

Kangaroo Island generally has subdued relief and mainly poor sandy soils.

Vegetation: "Eudesmia" - "Monocalyptus" - "Symphyomyrtus" sclerophyllous shrubland is typical of the Eyre and Yorke Peninsulas and Kangaroo Island while "Symphyomyrtus" - "Monocalyptus" forest is typical of the Mount Lofty Ranges. Extensive salt marsh and mangrove systems occur along and at the head of Gulf St Vincent and Spencer Gulf. The mangrove thickets comprise only one species: *Avicennia marina* var. *resinifera*.

28. Riverina.

Climate: Subtropical dry type (III) tending to transitional type with winter rainfall (IV) in the southern parts.

Physiography and Geology: Flood plains of the Murray and lower Darling Rivers and their major tributaries are the typical features of the Riverina landscape. Coarse deposits of sand and gravel are found in the eastern part of the region, tending to finer alluvial deposits in the west. Many of these deposits have been left by rivers of much greater flow from earlier times.

Vegetation: "Eudesmia" - "Monocalyptus" - "Symphyomyrtus" sclerophyllous shrubland occurs in the southeastern part of the region, grading to *Atriplex* - *Maireana* semi-succulent shrubland in the north. Along the rivers *Eucalyptus camaldulensis* forms dense forests, culminating in the well-developed forests of the Murray River flood plain. In the east, an increasing number of rocky rises carry "Symphyomyrtus" - "Monocalyptus" forest with considerable *Callitris* in the understorey. Heavy, dry, seasonally inundated soils carry "Symphyomyrtus" woodland.

29. Otway.

Climate: Warm temperate (V) with pronounced winter rainfall.

Physiography and Geology: This region has three major features: Recent (Quaternary) deposits in the west, uplifted sedimentary deposits of the Otway Ranges in the southeast

and a plain formed from lava flows to the north. Small volcanic cones are a feature of this landscape, as are the lake-filled volcanic craters. Some of the larger lakes were formed by faulting and subsequent volcanic activity preventing drainage. North of the lava plains are the western remnants of the Great Divide, which end in the Grampians and Dundas Tableland of western Victoria.

Vegetation: Dry, tussocky *Stipa* grassland was the typical vegetation of most of the lava country, with occasional pockets of woodland and forest in the wetter depressions. Since settlement, much of the grassland has been replaced by exotic pasture grasses. In the southeast, "Eudesmia" - "Monocalyptus" - "Symphyomyrtus" sclerophyllous shrubland is the typical vegetation type, grading to "Symphyomyrtus" - "Monocalyptus" forest on the hills and slopes of the ranges to the north. The Otway Range similarly has forests, some of which are dominated by very tall *Eucalyptus regnans* and *E. globulus*. Small patches of *Nothofagus* rainforest are found in the wetter valleys.

30. Howe.

Climate: Transitional with mainly winter rainfall (IV) to Warm temperate type (V).

Physiography and Geology: This region is complex, with coastal plains of recent origin to ranges with the highest peaks in Australia (Australian Alps). Much of the highland shows evidence of Pleistocene glaciation.

The Australian alps are a very even rolling plateau, resulting from a slowly uplifted peneplain. Lava flows were associated with the uplift activity, resulting in basalt plains on some of the higher areas (Mt Hotham, Dargo High Plains). Geologically this region is very complex, with a range of rock types forming the ranges and flat "tablelands".

Vegetation: At the highest altitudes small areas of alpine herbfield occur, interspersed with *Sphagnum* raised bogs and snow-fed streams. Much of the area regarded as alpine, however, is covered by "Monocalyptus" woodland (*Eucalyptus pauciflora*). Steeper slopes of the sub-alpine region carry "Symphyomyrtus" - "Monocalyptus" forest. In the south, wetter lowland valleys carry *Nothofagus* rainforest, while the foothills and plains carry "Corymbia" - "Monocalyptus" - "Symphyomyrtus" forest made up of complex mixtures of species, varying with altitude and elevation. Species-rich low shrubland is typical of the coastal fringe. In the eastern part of the region deep lowland valleys support the southernmost remnants of sub-tropical rainforest. The bays and estuaries support Australia's most well-developed salt marsh, often with extensive mangrove thickets, dominated by *Avicennia marina* var. *resinifera*. This latter species reaches the most poleward locality for any mangrove species at Corner Inlet, Victoria.

31. Nepean.

Climate: Warm temperate type (V).

Physiography and Geology: This whole region has resulted from erosion and uplift on a geological basin from Permian times. Many of the rocks were sandstone, with the northern part of the region inundated by lava flows during the late Tertiary.

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The most resistant remnants of this geological history remain as the Barrington Tops in the northeast and the Warrumbungle Range in the northwest. To the coast, rivers have eroded deep gorges in the sandstone and Pleistocene rises in sea-level drowned many coastal rivers.

Vegetation: "Corymbia" – "Monocalyptus" – "Sympphyomyrtus" forest forms the major vegetation cover of the hills and ranges. As in the Howe Region, the species which occur depend on elevation, slope, altitude and parent rock. Towards the coast a complex of lakes, dunes, drowned valleys and sandy plains carry a mixture of shrublands, low dense forests and wetlands. Large areas of the sheltered embayments and lower estuaries carry extensive mangrove and saltmarsh swamps.

32. McPherson.

Climate: Warm temperate type (V) transitional in the north to Tropical type (II), with some winter rainfall.

Physiography and Geology: In the east the region has coastal lowlands of varying width, with steep ranges rising behind, giving way to tablelands in the west. The ranges, which consist of sedimentary deposits, have extensive basaltic flows and granitic intrusions in the northwest. Steep gorges channel rivers from the tableland through the ridges to the coastal lowlands.

Vegetation: High rainfall and basaltic soils have enabled strong development of subtropical rainforests on the eastern edges of the ranges, with *Nothofagus* rainforest occurring on the higher plateaus. The tablelands and gentle western slopes of the ranges carry increasingly open "Corymbia" – "Monocalyptus" – "Sympphyomyrtus" forest. The complex of environments and climatic transitions account for a high level of species richness. This region was identified by Burbidge (1960) as a major "interzone" of species typically Australian and those with strong affinities to the Indo-Malayan Region to the north. Modern biogeographic researchers have confirmed her view.

33. Tasmania.

Climate: Warm temperate (V) in the west grading to transitional with winter rainfall in the east (IV).

Physiography and Geology: Apart from small areas in the alpine regions of the mainland (Region 30), Tasmania has the areas which experienced most glacial activity during the Pleistocene.

During the Jurassic much of Tasmania was affected by dolerite intrusions into existing sediments. These erosion resistant layers now cap the plateaus of the centre and east of the island. Younger deposits, from the Tertiary period, form the lowlands in the north.

Melting of the ice caps in the Pleistocene resulted in the inundation of Bass Strait and so Tasmania was separated from the mainland only in recent times.

Vegetation: Tasmania has a number of unique vegetation features: large areas of temperate rainforest dominated by *Nothofagus* and conifers (many of which are restricted to small isolated populations); extensive plains dominated by a tussock sedge (*Gymnoschoenus*) in the wet western regions; areas of alpine vegetation which share species and genera with New Zealand rather than the mainland. Tasmanian vegetation also has large numbers of endemic species. Many alpine and western rainforest vegetation types include species of conifers typical of genera and families dominant across Australia in the early Tertiary, but now existing only in relict populations.

The northern, central lowland and the eastern coastal areas are comparable with mainland Regions 29 and 30. "Sympphyomyrtus" – "Monocalyptus" forest is the major formation, giving way to species-rich shrublands on the exposed coastal fringes.

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5. MAJOR COMPONENTS AND DISTRIBUTIONS OF THE TERRESTRIAL FAUNA

H. HEATWOLE

INTRODUCTION

The Australian terrestrial environment is diverse. The climate varies from moist tropical and monsoonal in the north to arid in the centre and west, Mediterranean in the southwest and cool temperate along the southeastern seaboard, grading to alpine at the higher elevations. Accordingly, vegetation ranges from tropical and temperate rainforest through various forest and woodland types to savannah, grassland and desert scrub (Specht, 1981; Chapter 4, this Volume).

Despite this diversity, many of the climatic and vegetative regions are peripheral and the vast majority of the continent is semi-arid or arid. Widespread aridity is probably the predominant single feature that most characterizes Australia. It probably began in the northwest or the centre in the Tertiary and progressively spread to envelop much of the central part of the continent (Beard, 1976; Lange, 1982).

Associated with aridity is the prevalence of fire, a phenomenon that probably began to be of major ecological importance in the Miocene, as progressive aridity developed. Fire constituted part of the environment in which Australia's biota evolved and it still has a profound effect (Recher & Christensen, 1981).

The Great Dividing Range provides some topographic diversity on the eastern coast, but the lofty mountains of other continents are absent and the general character of the landscape is one of slight relief (Nix, 1981).

Another characteristic of the Australian environment is the general deficiency of nutrients (especially phosphates) in the soils, a condition to which the Australian sclerophyllous biota is highly adapted (Beadle, 1966; 1981). The fauna of Australia must be viewed in the perspective of these features.

GEOLOGICAL HISTORY

Throughout its geological history, Australia has been partially covered by seas, has moved through different latitudinal belts, suffered changes in climate and has been variously isolated from, been in proximity to or formed part of other land masses. This history has resulted in an extant fauna of widely different geographic origins, modes of adaptation and lengths of residence in Australia.

Pangaea

In ancient times, all the continents were aggregated as the single landmass of Pangaea (Fig. 5.1). By the middle of the Jurassic (about 160 mybp), however, the large Tethys Sea partly divided Pangaea into a northern supercontinent called Laurasia and a southern one, Gondwana. Laurasia later fragmented into North America, Europe and part of Asia and Gondwana into the remaining more southerly land masses (Estes, 1983).

Gondwana

Gondwana remained intact until the Early Cretaceous. At that time Australia was broadly in contact with Antarctica, more narrowly so with India and, indirectly through those two continents, with South America and Africa. There also were small landmasses included in Gondwana: New Zealand, New Caledonia, Madagascar and some of the Pacific islands (Fig. 5.2).

There was undoubtedly regional faunal divergence within Gondwana, just as there is today in different regions of any continent. Those parts most distant from the regions now represented by Australia would more likely have shown greater faunal divergence from Australia than geographically closer areas, subject of course to modification by effects of topography and of climatic or vegetational zonation within the super-continent.

Whatever these pre-breakup faunal geographical differences, the sequence in which various land masses fragmented would have influenced markedly the degree of faunal relatedness among the present derivative continents. India was the first to break away, northwards at the beginning of the Cretaceous (about 140 mybp). Africa followed soon thereafter (about 120 mybp). New Zealand moved away about 80 mybp leaving an axis of Australia-Antarctica-South America (Powell *et al.*, 1981; Keast, 1981c; Archer, 1984a). Australia did not break away from Antarctica until about the Late Paleocene (less than 60 mybp). From this sequence, one would expect that Australia would have the least faunal similarity (among taxa of Gondwanan origin) with India and Africa, but with greater affinity in increasing order with New Zealand, South

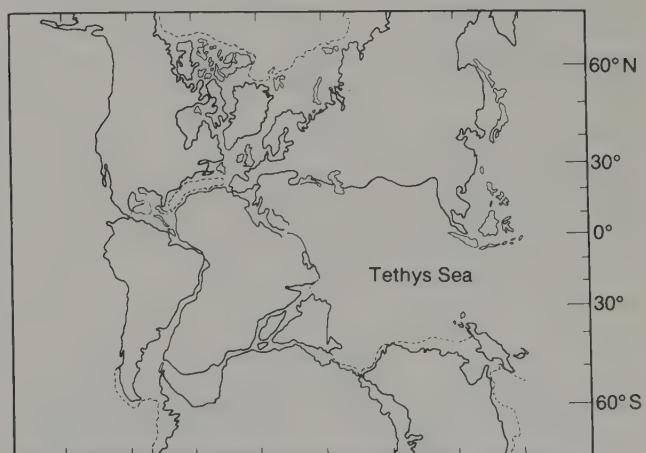


Figure 5.1 The continent of Pangaea as it appeared in the Early Jurassic (Mercator Projection). Dashed outline represents outlines of ancient continents. Solid lines indicate present continental outlines. Dot indicates South Pole. Only broad outlines indicated; outlines of epicontinental seas or of possible archipelago of Antarctic mainland ignored. [L. Bridges]

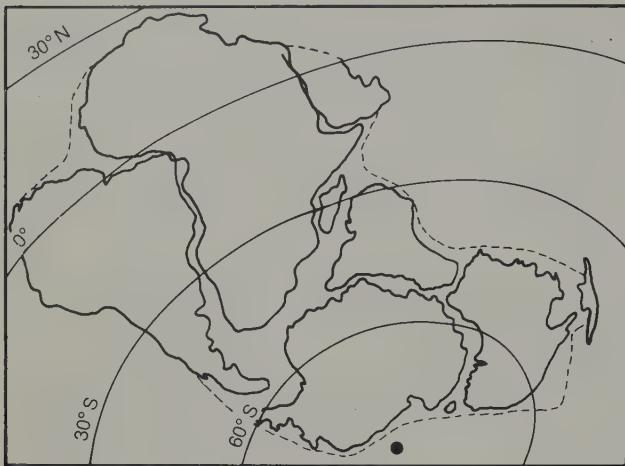


Figure 5.2 Gondwana as it appeared in the Early Cretaceous (Oblique projection). Dashed outline represents outlines of ancient continents. Solid lines indicate present continental outlines. Dot indicates South Pole. Only broad outlines indicated; outlines of epicontinental seas or of possible archipelago of Antarctic mainland ignored.

[L. Bridges]

America and Antarctica. The special circumstances of Antarctica, now largely ice-covered and inimical to most terrestrial life, combined with a rather meagre available fossil record, make a test of the degree of its relationship with Australia tenuous. These circumstances, however, do not apply to the other continents derived from Gondwana and, in general, the predictions are fulfilled. Australia and South America have the greatest faunal affinity, despite having been on opposite sides of Gondwana. There is less faunal similarity between Australia and either India or Africa. There are, however, particular groups in which Australia shows greater affinity with Africa and India than with other southern continents. These may have been distributed only in the northern part of Gondwana. If so, present affinities may reflect ancient regional distributional patterns within Gondwana. Keast (1981c) suggests that when Australia began to drift northward it contained the vestiges of an older (Paleozoic and Mesozoic), northern, subtropical, Gondwanan biota with African and Indian relationships and a newer (Eocene), southern and more cold-adapted one with affinities with Antarctica and South America. These various continental relations are discussed in relation to particular taxa below.

The Northward Migration

After separation from Antarctica, Australia spent more than 20 million years moving northward through a span of about 30° of latitude (Fig. 5.3) (Crook, 1981). During that time, it was relatively isolated from all other major landmasses and would not have been expected to receive new terrestrial taxa from outside sources except by long-distance oceanic dispersal. Consequently, one would predict that during the northward movement of Australia, the land fauna would be characterized by a divergence of the Gondwanan fauna from that of other southern continents, with little or no input from elsewhere. Faunal change would have occurred mainly by *in situ* evolution rather than from exchange with other places.

The extent of change in the isolated, ancient fauna may have been rather great. The movement of Australia northward was accompanied by passage through different climatic zones and there were major alterations in the patterns of wind systems and the circulation of ocean currents.

The Paleocene climate of Australia, while the latter was connected to Antarctica or shortly after separation, is problematical and opinions vary from cool to warm temperate with a high rainfall (Kemp, 1981) to subtropical or tropical (Lange, 1982). During the Eocene, Australia maintained widespread humid tropical conditions, even in the south, but cooled toward the end of the epoch. The Oligocene in Australia was characterized by marked cooling, especially at high latitudes, as well as by a reduction in rainfall. Parts of Australia probably were relatively arid. In the Early Miocene there was a warming; conditions were relatively moist. In Middle to Late Miocene (about 12 to 15 mybp), however, there was a rapid expansion of the Antarctic ice sheet. Conditions became colder and rainfall decreased; central and northwestern Australia became dry. In the Pliocene, there were wide fluctuations in climate. There seems to have been a brief, warm, moist period in the Early Pliocene, followed by progressive aridity and perhaps coolness over most of the continent, with wetter and warmer conditions perhaps persisting in southern coastal regions. The Pleistocene saw worldwide fluctuation in sea-level and climate associated with alternating periods of glaciation (glacials) and glacial retreat (interglacials) at higher latitudes and altitudes. In general, the aridity of the Late Miocene and much of the Pliocene continued through the Pleistocene, although there was considerable fluctuation in climate, from wetter and warmer interglacial conditions to cooler and drier glacial ones (Bowler *et al.*, 1976; Frakes *et al.*, this Volume; Galloway & Kemp, 1981).

Associated with the rather rapid fluctuations in climate in the Tertiary and Quaternary were corresponding changes in vegetation (Smith, 1982; Lange, 1982; Singh, 1982). During the earlier, warm and moist periods, tropical and subtropical rainforests were widespread in Australia, but temperate forests and rainforests predominated in the cooler moist periods. With the generally progressive aridity in the Tertiary, there was a shift to grassland and xeric vegetation, with pro-



Figure 5.3 Position of the southern continents in the Eocene (South Polar stereographic projection). Arrows indicate paths of movement of continents. Dashed outline represents outlines of ancient continents. Solid lines indicate present continental outlines. Dot indicates South Pole. Only broad outlines indicated; outlines of epicontinental seas or of possible archipelago of Antarctic mainland ignored.

[L. Bridges]

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nounced regional differences (Lange, 1982). Aridity was most pronounced in the centre and west and moister conditions prevailed toward the eastern, southeastern, southwestern and part of the northern periphery. All of these climatic and vegetational changes undoubtedly affected the adaptive radiation and evolution of the Australian fauna.

Contact With Asia

With the approach of Australia towards southeastern Asia in the Miocene, the long period of isolation came to an end. As the distance between the two plates closed, the likelihood and frequency of overwater dispersal of fauna would have increased; one would predict an increasing impact of the Asian fauna upon the Australian one.

The marked climatic and sea-level fluctuations of the Tertiary and Quaternary undoubtedly influenced the immigration of Asian fauna into Australia, the likelihood of their establishment upon arrival and the subsequent course of their distributional spread and adaptive radiation.

Based on the above geological scenario, one would predict that the Australian terrestrial fauna is a mixture of two major elements, an ancient one derived from Gondwana (and with an affinity with South America) and a vastly more modern assemblage with southeastern Asian affinity. This theory has the support of data from various taxa.

THE FAUNAL ELEMENTS

The present terrestrial faunal elements in Australia can be divided into five categories. The oldest two contain those taxa that are relicts from former, larger continents and are referred to as the **Pangaean Element** (Archaic Element) and the **Gondwanan Element** (Old Southern Element).

Those more recent taxa with an Asian origin can be subdivided according to the time of their arrival in Australia. The oldest members of this group began to appear in the Tertiary fossil record and, therefore, have had considerable time to undergo adaptive radiation within Australia. These are designated as the **Asian Tertiary Element**. Later arrivals, in the Pleistocene and Recent, although of ultimate Asian derivation, primarily have a more specific local origin such as New Guinea or Timor. They will be called the **Modern Element**.

The fifth category, the **Introduced Element**, includes those species introduced by man. Obviously, these are newcomers to the Australian scene and have not adaptively radiated within Australia. Their distribution and success depends partly upon the extent of their preadaptation to existing local conditions rather than upon evolution in an Australian historical and climatic context and partly upon human modification of Australian environments. Their regions of origin are various.

Pangaean Element (Archaic Element)

There are Australian animal groups that are represented in the fossil record of various continents, including northern ones, prior to the mid-Jurassic break up of Pangaea, or whose present distribution and primitive status suggest that they were distributed widely in Pangaea and that their present occurrence in Australia dates from the time Australia was a part of Pangaea. A continuous residency in Australia since Pangaean times is implied. These animals constitute the most ancient of the terrestrial faunal elements of Australia. Often, their worldwide distribution is disjunct and isolated

relicts occur in widely separated localities on different continents, extinctions having long since occurred in the intervening areas.

If extinction of a Pangaean group was widespread, leaving representatives on only a few southern continents, and if that group was soft-bodied and not easily fossilized, there might be difficulty determining if that group was part of the Pangaean rather than the Gondwanan Element. The Onycophora, for example, has no fossil record and is now primarily on southern continents or peripheral to them. Their primitive structure and undoubted antiquity place them in the Pangaean Element. Other Australian groups of Pangaean origin are the Symphyla, Diplura, Blattodea (cockroaches), the relict ant *Nothomyrmecia*, the Tasmanian endemic spider family Hickmaniidae, mecopterans of the family Meropidae, the fly genus *Nemopalpus*, the beetle genera *Cupes* and *Rhysodes* (Mackerras, 1970) and the earthworm tribe Acanthodrilini (Main, 1981b). Note that many of these examples are at the higher taxonomic levels.

The distribution of Pangaean taxa within Australia has no consistent pattern. Time, subsequent adaptive radiation into new habitats and extinction over large parts of the continent have obliterated original distribution patterns, except perhaps for some relicts maintained in ancient refugia.

Gondwanan Element (Old Southern Element)

Several animal groups (1) have fossil records extending back to Gondwanan times, (2) have their closest relatives in other continents of Gondwanan origin with no, or very distant, relatives in Asia or other northern continents, (3) are primitive and found only in Australia or (4) have some combination of the above. Examples are marsupial mammals, ratite birds, chelid turtles, diplodactyline geckos, megascolecine earthworms, terrestrial molluscs of the families Athoracophoridae, Cystopeltidae, Megaspiridae, Rhytididae, Bulimulidae and Acavidae, spiders of the taxa Hexathelinae, Migidae and Actinopodidae, many insects, the scorpion genus *Cercophonius* and several genera each of Opiliones and Pseudoscorpionida (Mackerras, 1970; Main, 1981c).

In contrast to the Pangaean fauna, many of the Gondwanan taxa are at the familial or generic level, rather than at higher ones.

The Gondwanan Element entered and developed in Australia at a time when the environment was relatively cool and humid. There has been considerable subsequent adaptive radiation and a number of taxa has become adapted to drier regions (for example, many marsupials, the mygalomorph *Missulena*, the snail *Bothriembryon*, some dynastine beetles, the pseudoscorpion genus *Astrochorus*) (Main, 1981c) or have invaded the tropical north. Many of the more sedentary and evolutionarily conservative taxa, however, tend to occupy the cooler, more humid regions in the southern part of the continent.

Asian Tertiary Element

Presence of a particular Asian taxon in Australia does not necessarily indicate a single entry and subsequent adaptive radiation from one established species. Nor is it likely that at any time in history was there a mass flow of all species of Asian taxa into a newly accessible Australia. The vagaries of overwater dispersal probably acted as a species filter.

As the Australian and Asian tectonic plates closed during the Tertiary, finally abutting, opportunity for invasion of Australia by an entirely new fauna became possible. This was, of course, not a momentary event. Continental drift is a very slow process, in the order of only about 60 mm per year

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(Archer, 1984a). One would expect that with closer approach there would be increasing frequency of overwater transport, the incidence varying greatly among taxa depending on their vagility and resistance to the conditions of aerial or flotsam transport. Overwater dispersal is fortuitous, relatively rare and, for a given taxon, may occur at widely spaced intervals. An early immigration and establishment by a particular taxon thus may have resulted in rather extensive adaptive radiation before a second invasion by another member of that same taxon. For a higher taxon (say family), there may have been multiple invasions, widely spaced in time and with the degree of speciation and adaptive radiation decreasing from the older to the newer immigrations. The older and more widely separated the different immigrations, the more easily can they be distinguished. With close contact between Asia and Australia and increased frequency of faunal exchange, such distinctions would become blurred. Examples of the Asian Tertiary Element include most families of lizards and snakes, the conilurine rodents, many birds, buthid and scorpionid scorpions, theraphosid spiders and many insects.

Modern Element

Whereas the break between the Gondwanan and Tertiary Asian Elements involves a gap of more than 20 million years, the distinction between the Modern and Tertiary Asian Elements, which are merely opposite ends of a continuum, is less marked. The separation, nevertheless, is useful and distributional patterns of the two elements may be quite different.

Taxa of the Modern Element have scarcely diverged, if at all, from their New Guinean or Indonesian relatives. Where there is divergence, it is usually only at the specific or subspecific level.

Selected examples include the ranid frog, *Rana daemeli*, the turtle *Carettochelys insculpta*, native rats (*Rattus*) and the Rainbow Bee Eater (*Merops ornatus*) as well as various spiders and insects.

Some modern immigrants with great powers of overwater dispersal, such as small arthropods carried as aerial plankton by wind, may come from sources other than Asia.

Comparison Of Elements From The North

One of the distinctions that might be made is that the oldest Asian immigrants have widespread Asian affinities. These sometimes are called the Old Northern Element and may be difficult to distinguish in some cases from Pangaean taxa. Later immigrants have a more restricted relation with the oriental part of Asia and are called the Oriental Element. By contrast, the Modern Element usually has a relationship specifically with (1) the secondary radiation that centred in New Guinea and whose Australian representatives occur in northeastern Queensland or only on Cape York or with (2) the Indo-Malaysian fauna, with the Australian representatives occurring in northwestern Australia and/or the tropical Northern Territory (Fig. 5.6).

There is good evidence in various taxa for successive waves of immigration with each wave having undergone different degrees of adaptive radiation.

Some of the presumably older taxa entered from the north, spread over the continent and then underwent adaptive radiation, often from secondary southern or central centres. A later wave of immigration by related taxa may not have spread so far or radiated to such a great extent, maintaining their ecological affinities with tropical conditions. Competition between members of the successive waves also may have had a limiting effect on distribution. The result is that some

of the older taxa of Asian origin are more southerly in distribution in Australia and have their greatest species richness there. Related taxa immigrating later are restricted to, or have their greatest diversity in, the north.

Reptiles. Australian representatives of the lizard families Agamidae and Scincidae and the snake family Elapidae have radiated secondarily from southern and Eyrean centres, whereas most varanids have remained primarily northerly in distribution (Cogger & Heatwole, 1981). Cogger (1961) postulates four agamid invasions of Australia, all via New Guinea, the first in the mid-Tertiary (*Moloch*), the second in the Pliocene (most of the Australian agamid genera) and the final two relatively recently. Those of Tertiary origin are adapted primarily to arid and semi-arid conditions, whereas the later invaders are found only in the wet, forested parts of eastern Australia. Witten (1983) recognizes only two groups, an older radiation and a group of newer arrivals. The varanids probably first entered sometime after the lower Miocene and radiated as the subgenus *Odatria* (of the genus *Varanus*) and its derivative *gouldii* species-group and were followed later, perhaps in the Pleistocene, by the *indicus* group (King & King, 1975).

Drosophilids. The fruit-fly subgenus *Scaptodrosophila* entered Australia from the north, but underwent speciation in the south and now is distributed there. Later subgenera of the genus *Drosophila* to arrive remained northerly in their distribution (Parsons & Bock, 1981).

Lepidoptera. There was a number of northerly incursions of papilionoid butterflies. Of the Nymphalidae, the subfamily Satyrinae probably entered first, as it has several southern centres of high species density, especially in Tasmania and the southeastern alpine and subalpine regions (Kitching, 1981). In contrast, the Nymphalinae is represented poorly in the south, but has high species densities in the north and may have resulted from a later wave of immigration. The families Riodinidae and Libytheidae are represented only by one species each in the far northern regions and must represent still later intrusions. The most recent immigrants are various species which have northern extrazonal distributions as well as occupying parts of northern Australia. Examples are *Cethosia penthesilia* (Indonesia to northern Australia) and *Tellervo zoilus* (New Guinea to Cape York).

Muridae. Native murid rodents seem to have reached Australia in three waves (Hand, 1984). The first rodents are referable to the tribe Conilurini which arrived in the Pliocene and subsequently radiated substantially in Australia (sometimes denoted "Old Endemics"). The second wave included the tribes Hydromyini and Uromyini which apparently radiated in New Guinea and then entered Australia within the last two million years. The genus *Rattus* subsequently entered within the last million years and diverged into the modern endemic species of this genus.

The older, southern taxa of Asian origin tend to have distributional ranges with a greater similarity to those of Gondwanan origin than to those of later Asian immigrants. They can be distinguished primarily by whether their phylogenetic affinities are with Gondwanan or Asian taxa.

To place successive waves into precise time scales is not always possible, but only relative to each other. The older ones almost certainly occurred in the Tertiary or earlier; the later ones may have been Tertiary or have occurred later and, thus, spill over into the Modern Element (see below). A major point of controversy at the present time is whether particular immigrations, and divergences within taxa, date back only to the Pleistocene changes in climate and sea-level or whether they reflect Tertiary events.



Figure 5.4 Zoogeographic regions of the world.

[L. Bridges]

Many of the affinities between the Asian fauna and Australian taxa of the Asian Tertiary Element are at the familial or generic level.

Introduced Element

The history of arrival and spread of the recent anthropochorous element is dealt with in Chapter 11 of this Volume.

DISTRIBUTIONAL PATTERNS

Each species has limits to its geographic distribution. The limiting factors may differ on the various edges of its range. One of the tasks of zoogeography is to identify what those limiting factors are and how they operate upon the species in question. The boundaries imposed by limiting factors may change in time and the distributions of species expand or contract accordingly. In extreme cases, extinction may occur. To assess the role of such changes upon the distributions of individual species is of considerable ecological interest and, if a species is of economic, medical or conservational significance, there may be practical importance as well. Valuable though such autecological information may be, it is important to try to generalize about animal distributions and to see if there are consistent patterns that can be interpreted in historical or ecological terms. Are there recognizable faunal regions in which the inhabitants are linked by similar past history or present environment? Or, alternatively, are species distributed each according to its own response to environment and history, but in a random way with respect to other species?

Of the six world Zoogeographical Regions (Fig. 5.4) the largest is the Palaearctic Region which includes Europe and most of Asia. The Nearctic Region consists of North America. These two together are often referred to as the Holarctic. South America and Central America collectively make up the Neotropical Region. Africa is the Ethiopian Region. The Oriental Region consists of India, southeastern Asia, the Philippines and most of the Indonesian archipelago. The

Australian Region includes the rest of that Archipelago, Australia, New Guinea and New Zealand, with declining affinities outward into the Pacific islands.

There are broader transition zones between regions than lines drawn on a map would suggest. Northern Africa and the Arabian Peninsula represent a transition between the African and Palaearctic Regions. Central America shows a grading of fauna between the Nearctic and Neotropical Regions and there is some overlap between the Oriental and Palaearctic Regions (Darlington, 1963).

At one time, the boundary between the Oriental and Australian Regions was considered a sharp one, represented by the Wallace Line (Fig. 5.5). Different authorities, however, have drawn the Wallace Line rather differently and several other lines, equally believed to separate the two regions, have been drawn by other zoogeographers (Muller Line, Weber Line and Lydekker Line) (Muller, 1974). The position of these lines depends on the dispersal abilities and ecological attributes of the taxa on which they are based and no single line serves equally well for all taxa. It is best not to think of a discrete boundary between these two regions (Keast, 1981c; Cox *et al.*, 1973), but rather to consider the area between the easternmost (the Lydekker Line) and the westernmost (the Wallace Line) of the proposed lines as a broad transition zone (Fig. 5.5) sometimes called Wallacea. The Australian faunal influence declines westward in this zone and the Oriental one attenuates eastward; the limits vary among taxa.

New Guinea occupies a special place in this scheme. When the Australian and Asian Plates collided, the leading edge of the former was the southern part of the island of New Guinea. The central mountains originated as a result of a collision of the two Plates in the Miocene and the entire mass pushed against some of the outlying islands of the Asian Plate (the Torricelli and Finisterre Islands) and incorporated them into the northern part of New Guinea. Thus, New Guinea had a three-fold origin: part of the old Australian Plate, old outlying Asian islands and newly formed mountains. The former two components already would have had their resident faunas, providing a mix of the two regional elements; the young mountains provided vacant, qualitatively

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Figure 5.5 The transition from the Oriental Zoogeographic Region to the Australian Region. Wallacea is the area between the Wallace and Lydekker lines. Within it there is a decline in Oriental elements from west to east and a decline in Australian ones from east to west.

different habitats from those either of the Australian or Asian components. This diversity stimulated a rapid and extensive radiation which formed an autochthonous element within New Guinea.

This Volume is not concerned directly with the fauna of New Guinea, but recognition of its tripartite origin and of the subsequent montane adaptive radiation within it, are necessary for an understanding of New Guinean influence on the Australian fauna (Tyler, 1979a).

Interior Versus Peripheral Distributions and Zoogeographic Subregions

Inspection of a large number of maps of the geographic ranges of Australian terrestrial species immediately suggests that there are two major kinds of distributional patterns, interior (arid-adapted) and peripheral (wet-adapted) (Figs 5.6 and 5.7). A few eurytopic species with sufficient ecological and physiological flexibility to cope with both kinds of environment are found throughout the continent, but the distribution of most clearly falls into one or the other of these general categories.

Within the above two general areas there is a variety of subordinate distributional patterns. Not all species with an interior distribution occur throughout the entire central portion of the continent; many occupy only part. Fragmentation is pronounced even more on the periphery. There are areas where the limits of a number of species coincide at least roughly and recognition of that has led to the delimitation of zoogeographic subregions within the Australian Region.

New Guinea and Australia have markedly different faunas and sometimes are designated as the Papuan and Australian Subregions, respectively, with further subdivisions (provinces)

denoted within Australia. Other biogeographers consider the subdivisions within Australia as subregions rather than provinces and this is the terminology followed here.

Researchers working on different taxa have contributed different schemes and terminologies (Moore, 1961; Kikkawa & Pearse, 1969; Keast, 1959; Horton, 1973; Littlejohn, 1981), each with strengths and weaknesses but all vaguely similar. The number of subregions proposed varies from three to 12. Some of these perhaps reflect the ecological peculiarities of the taxa on which they were based and some of the finer subdivisions, especially, do not seem widely applicable.

No one scheme would fit all taxa and, obviously, even within a given taxon certain species may be effectively blocked by barriers that have little impact on others. There are species that have very narrow tolerances or specific requirements that limit them to extremely local, specialized situations and they will have ranges that do not cover an entire subregion. There are features of climate or topography, however, that serve as a barrier to many taxa and mark the limits of the ranges of many species.

The following are the general subregions most commonly accepted and most generally applicable (Fig. 5.8).

In the moist, tropical north, the western Timorian Subregion is separated from the eastern Torresian Subregion by a seasonally semi-arid tract at the base of the Gulf of Carpentaria. Down the eastern seaboard is a moist, subtropical to temperate area, the Kosciuskan Subregion. It is bounded on the periphery by the ocean and inland by the Great Dividing Range and increasing aridity. The boundary between the Kosciuskan and Torresian subregions has been set at various places. One such demarcation coincided with the Clarence River in northern New South Wales, a boundary rejected by Horton (1973) in favour of the semi-arid gap in the Towns-

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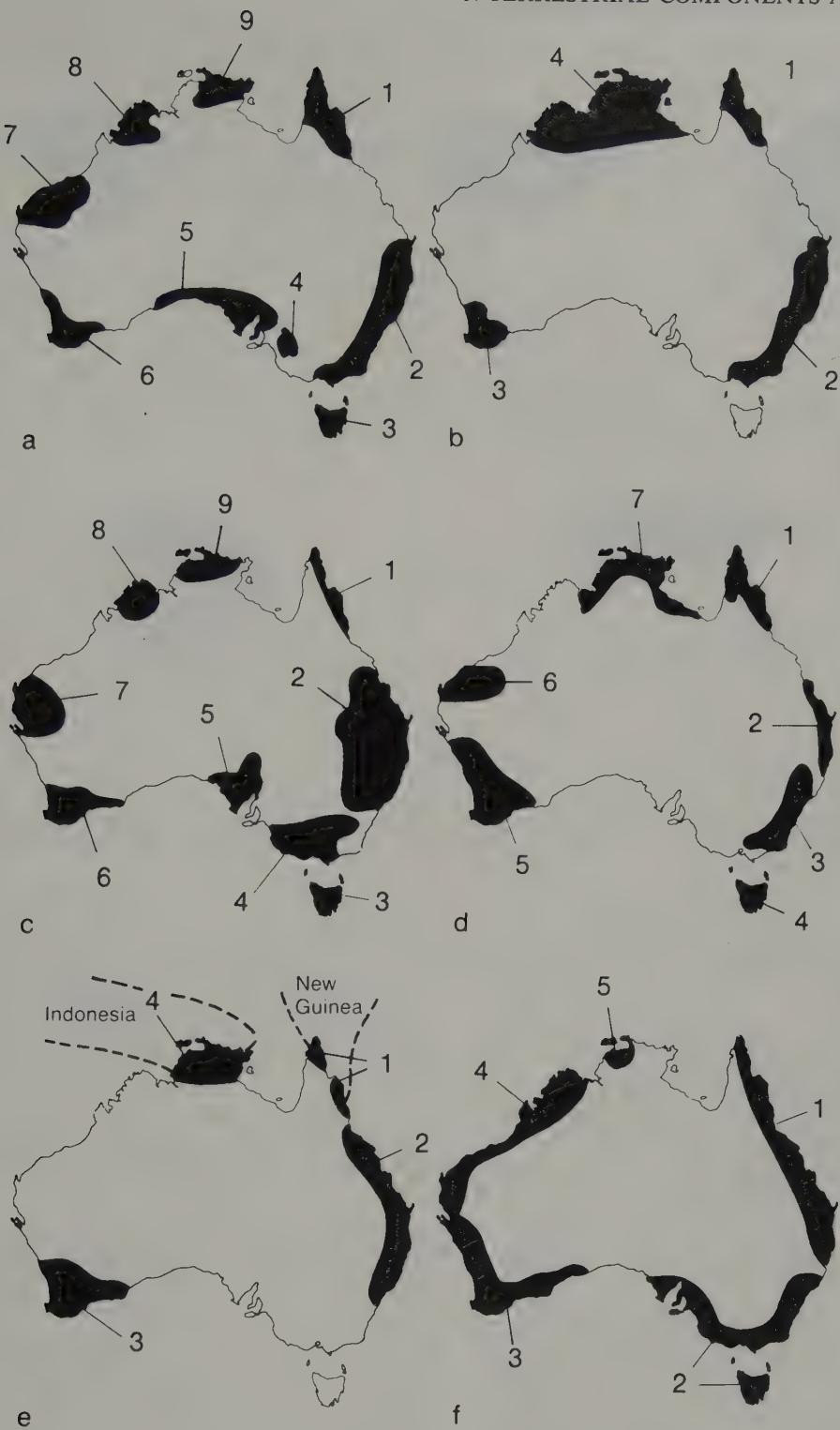


Figure 5.6 Examples of peripheral distribution of species or genera of terrestrial animals in Australia. (Data from Mackerras, 1970; Key, 1976; Koch, 1977; Cogger, 1979; Main, 1981a; Bishop, 1981; Kitching, 1981; Keast, 1981b; Common & Waterhouse, 1981; Strahan, 1983; Blakers *et al.*, 1984).

- a. MAMMALS: 1. *Nycticeius sanborni*; 2. *Trichosurus caninus*; 3. *Sarcophilus harrisii*; 4. *Pseudomys apodemoides*; 5. *Lasiorhinus latifrons*; 6. *Macropus irma*; 7. *Ningauia timealeyi*; 8. *Wyulda squamicaudata*; 9. *Antechinus bellus*.
- b. BIRDS: 1. *Ramsayornis modestus*; 2. *Climacteris erythrops*; 3. *Eopsaltria georgiana*; 4. *Platycercus venustus* (= *eximilus* northern race).
- c. REPTILES: 1. *Liassis amethistinus* (= *Morelia amethistina*); 2. *Pseudechis guttatus*; 3. *Leiolopisma pretiosum*; 4. *Delma impar*; 5. *Amphibolurus fionni*; 6. *Drysdalia coronata*; 7. *Lerista nichollsi*; 8. *Lerista borealis*; 9. *Sphenomorphus douglasi*.
- d. AMPHIBIANS: 1. *Rana daemeli*; 2. *Crinia tinnula*; 3. *Litoria citropa*; 4. *Crinia tasmaniensis*; 5. *Pseudophryne guentheri*; 6. *Pseudophryne douglasi*; 7. *Litoria tornieri*.
- e. INSECTS: 1. *Tellervo zoilus* (hamadryad butterfly); 2. *Dasybasis cirrus* (a tabanid fly); 3. *Swanea* (a genus of morabine grasshoppers); 4. *Cethosia penthesilia* (Orange Lacewing Butterfly).
- f. MISCELLANEOUS INVERTEBRATES: 1. *Isometrus melanodactylus* (scorpion); 2. *Stanwellia* (spider); 3. *Bothriembryon* (snail); 4. *Rhagada* (snail); 5. *Urodacus exellans* (scorpion).

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Figure 5.7 Examples of interior distributions of species or genera of terrestrial animals in Australia. (Data from Cogger, 1979; Keast, 1981b; Bishop, 1981; Strahan, 1983; Blakers *et al.*, 1984). 1. *Macropus rufus*; 2. *Stipiturus ruficeps*; 3. *Ctenotus quattuordecimlineatus* (a skink); 4. *Notaden nichollsi* (a frog); 5. *Sinumelon* (a snail).

ville-Mackay area, which not only marks a barrier but accords with distributional patterns. This is the northern boundary accepted here.

Littlejohn (1981) points out that in the Kosciuskan Subregion there is a transition from a preponderance of summer rainfall in the north to a predominance of winter rainfall in the south, with an intermediate zone of seasonally uniform rainfall (Fig. 5.8). This factor, along with its rather large altitudinal and latitudinal extent, gives the Kosciuskan Subregion considerable internal heterogeneity and distributional subgroupings.

The cool, temperate Tasmanian Subregion is restricted to Tasmania and, thus, is insular.

The Southwestern Subregion is located on the southwestern corner of the continent in an area of Mediterranean climate. It is bounded peripherally by the sea and inland by aridity. The Nullarbor Plain forms an extensive gap isolating it from the Kosciuskan Subregion. The final Subregion, the Eyrean, is the largest and incorporates the dry interior of the continent. It is bordered by the sea in the west and along the Great Australian Bight and where narrow tongues of aridity reach the coast elsewhere. Otherwise, it is bordered by the moister areas of the other subregions.

The major modifications of this scheme have been: the inclusion of the Timorian in the Torresian Subregion; the combination of the Kosciuskan and Tasmanian (and sometimes the Southwestern) into a single subregion called the Bassian; the setting of different boundaries between the Torresian and Kosciuskan Subregions; the addition of another subregion along the western coast; the insertion of some other subregions into the transitional gaps between those of the present scheme; or, as mentioned above, the addition of a variety of other regions applicable only to particular taxa.

Refinement beyond the scale of the scheme presented here may be possible and a greater number of subregions erected to reflect the influence of minor barriers on some species or the local effect of slight variation in climate. Such refinements are left for individual treatment in the forthcoming volumes.

These subregions reflect present distributions and barriers. The barriers of the past were different and had a profound effect on the Australian fauna. The effects of temporal shifts in the environment are described below.

There have been botanical regions proposed, just as there have been zoological ones. Since plants are an important structural and trophic component of the habitat of many animals, and since both kinds of organisms respond to climatic and topographical factors, it might be expected that there would be a certain amount of congruence between botanical and zoogeographical regions. Although it is beyond the scope of the present book to dwell on the strictly botanical aspects, it is instructive to compare patterns based on the two major kinds of organisms. Barlow (1984) proposed a delineation of botanical regions for Australia, which he (1985) later modified, largely in response to criticism by Beard (1985). The revised scheme referred to natural regions, rather than botanical ones alone, as criteria in addition to plant distributional patterns were considered. In all, 33 natural regions were recognized. They cannot be discussed in detail here, but the six major floristic zones in which they were grouped, correspond remarkably closely to the zoogeographic subregions described above. These 33 natural regions are described in Chapter 4.

Barlow's (1985) Northern Zone is roughly equivalent to the Timorian Subregion, the North Eastern Zone to the Torresian Subregion, the South Eastern Zone to a combination

of the Kosciuskan and Tasmanian subregion (Bassian) and the South Western Zone to the Southwestern Subregion. Two of the natural zones in combination (Western Shield and Eyre-Murray Basin) correspond to the Eyrean subregion.

Horton (1973) points out that subregions established solely on the basis of clustering of boundaries of animal distribution resulted in nearly the same geographic divisions as occurred when the bases for mapping were climatic and physiographic barriers. The same seems to be true in relation to plant distributions. Congruence of these approaches inspires confidence in the usefulness of the concept. The resultant general patterns recognize the relationships between animal and plant distributions and between those and environmental influences. At the same time, departures from general patterns highlight distributional idiosyncrasies of particular taxa and may lead to greater insights into the environmental factors affecting them.

Relation To Vegetation Type

Many species of animals are characteristic of a particular vegetation type and may even be restricted to it. Often, the reasons for such a one-to-one correspondence are not clear, but possible explanations include (1) dependence on a food plant restricted to species in that formation, (2) behavioural responses to the unique structural configuration provided by the vegetation (perhaps related to shelter or nest sites), (3) response to associated microclimates, (4) restriction to the same geographic region as the vegetation through common susceptibility to limiting factors, or (5) dependence upon another animal species (perhaps for prey) which is in turn linked to the vegetation in one of the above ways.

Historical considerations also may be important. Tindale (1981) suggests that the Lepidopteran family Agathiphagidae could have evolved at the beginning of the Jurassic or earlier and that its origin may have been linked with such primitive plant groups as the Araucariaceae, which still serves as a food source. He further suggests that the evolution of other Homoneura (given the increasing evidence of their antiquity) may have been associated with ferns and conifers, as some still are, but that the Heteroneura, or more advanced lepidopterans, have a primary association with the expansion and radiation of the angiosperms in the Cretaceous. Howden (1981) suggests that the evolution of the higher families of beetles also is related to the radiation of angiosperms.

The evolution and distributions of various insects and their host plants probably have had historical links that are reflected in the present; others show more flexibility in preferences for host plants.

Animal distributions probably are influenced by many environmental features and no blanket statement can be made. Yet, to emphasize the possible primacy of vegetation as a correlate (if not necessarily a cause) of distributional patterns of animals is not unreasonable. Certainly, analyses of the faunas of particular kinds of vegetation and faunal comparisons among different vegetation types are important exercises. Parsons & Bock (1981), for example, found that Australian *Drosophila* subgenera fall into two groupings. An older invasion radiated in the south and inhabits temperate (or at best subtropical) forests; these species do not come to fruit baits. Species of a newer invasion, restricted to the humid forests of the north, do come to fruit baits. The tropical forests have resources of fleshy fruits that the southern ones lack. Thus, food resources may account, at least in part, for this clear separation by forest type.

There have been few Australian studies of complete faunas of particular vegetation types. Many lists of species of particular taxa for various localities or stands of vegetation have been



Figure 5.8 Zoogeographic subregions of Australia. = area of winter rain. = area of seasonally uniform rain. = area of summer rain.

produced and the increasing popularity of "environmental impact" and "baseline" studies is generating many more such superficial, local approaches to faunal study. These will provide raw data from which future valuable syntheses can be constructed.

There is good information on the relation of some taxa to vegetation and some localities have been surveyed for a few taxa. Seldom has the complete fauna of a particular kind of vegetation been examined on an Australia-wide basis.

A study which can serve as a model of what can be done in this regard is that of Kikkawa *et al.* (1979) on the vertebrate fauna of Australian heathlands. The authors examined each of the terrestrial classes separately and indicated a series of grades of association of species with heathland habitats. They were, in decreasing order of restriction to heathland:

- 1) Phylogenetic and geographic relicts showing a high degree of specialization in the heathland habitat and confined to southwestern Western Australia, the possible result of radiation at a time of heathland dominance and subsequent extinction of all or most allied forms.
- 2) Phylogenetic relicts showing a high degree of sedentariness and adaptation to ground-living in dense cover, remaining otherwise unspecialized morphologically and having lost links with modern forms.
- 3) Species showing a relict pattern of distribution in heathlands as a result of phylogenetic and geographic isolation after radiation into heathlands at a time of heathland dominance.
- 4) Major taxa showing specialization as nectar-feeders as part of their heathland adaptation and geographic radiation at the time of heathland dominance, but subsequent secondary adaptation to "escape" from dependence on heathlands; some species of these groups still show association with heathland without exclusive dependence on this habitat.
- 5) Genera showing radiation during arid periods, with some members inhabiting heathlands.
- 6) Genera showing radiation in a wide range of modern habitats including heathlands as an adaptive zone.

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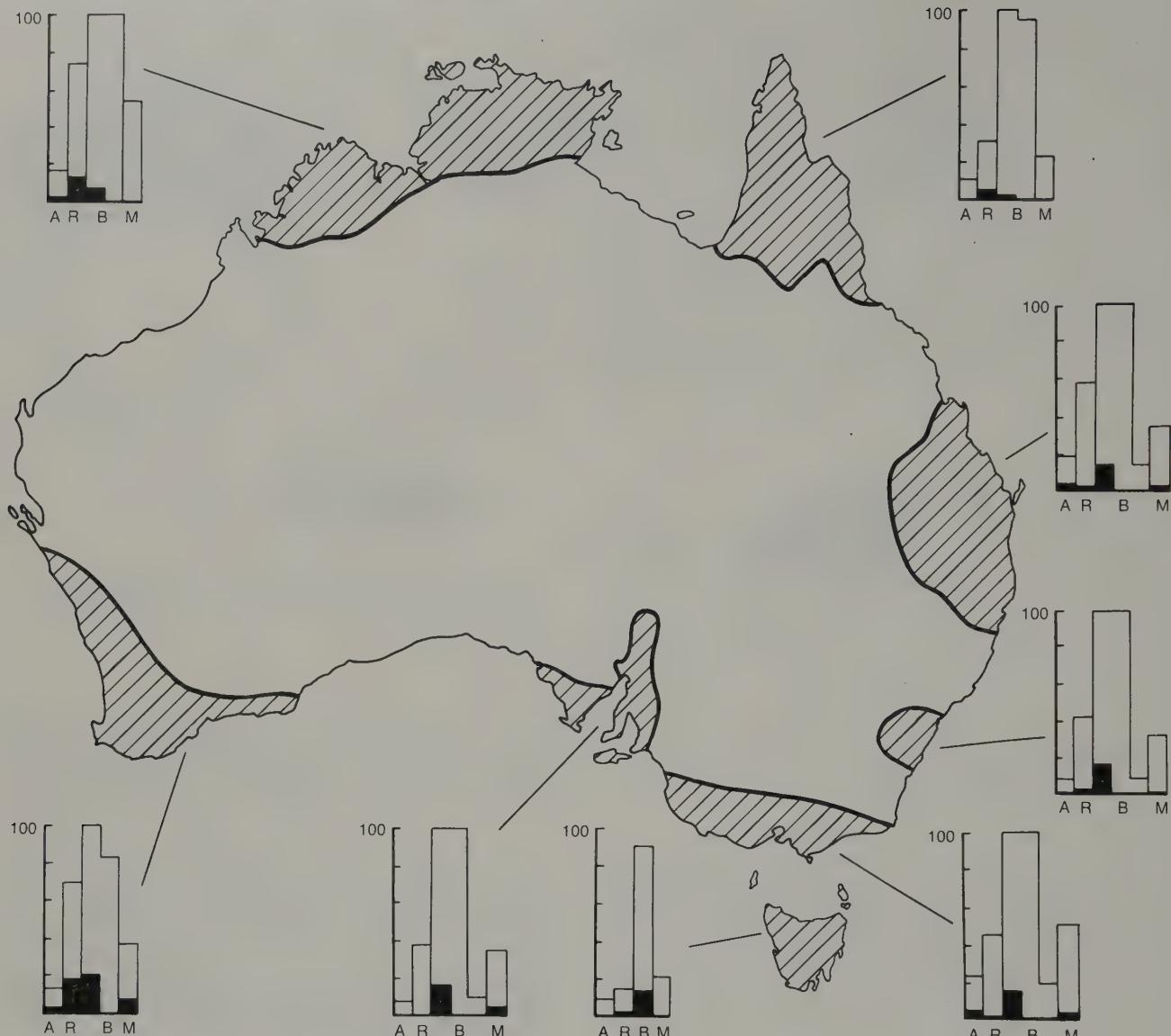


Figure 5.9 Map of major regions containing heathlands (cross hatched) in Australia. Histograms show the number of indigenous species of vertebrates known from heathlands for each area (white) and with special association with heathland (black). A = amphibians. R = reptiles. B = birds. M = mammals. For birds numbers greater than 100 can be read by summing the columns. (After Kikkawa *et al.*, 1979)

7) Species showing recent adaptation to coastal heathlands in parts of their range.

8) Species showing no obvious association with heathlands.

An important part of this study was the linking of specific animal taxa with the history of heathlands and to show how intertwined were the fates of vegetation and animal life. Heathland habitats are now fragmented in Australia, but were once extensive. Through the Tertiary, heath increasingly became restricted to coastal or subcoastal refugia and in the Quaternary invaded coastal and inland dunes.

The patterns of different degrees of restriction of the fauna reflect this history. Some of the old fauna, already adapted to heathlands, were unable to radiate into other habitats and their distributional history has followed that of the heaths, becoming more narrowly restricted and fragmented. Other taxa were able to adapt to changing conditions and some of their component species moved out to new habitats as those arose. During the ever-shifting dynamism of environmental

change, adaptation in the reverse direction also occurred, some species of otherwise non-heathlands taxa becoming adapted to heathlands. This process of radiation into or specialization within the heathlands is still continuing.

Specialization was found not to be limited to relict species but to be a continual process involving taxa from the oldest to the most recent heathland colonizers. Specialization to heathland living seems to have occurred many times with different chronologies for different taxa.

Two findings of this study deserve further comment. The first is that the majority of vertebrate species recorded from heathlands occur more commonly in other habitats (Fig. 5.9). This casts doubt upon the paramount importance of this vegetation type as a direct determinant of distributions for most species. Other vegetation types with a greater proportion of specialists may exert a greater effect.

The second is that both ends of the sequence in relative specialization and restriction to heathlands involved a variety of taxa. The most specialized and restricted species were

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often older, relictual and monotypic (at generic or familial level) forms, but of various taxa. Category 1 contained a frog, a turtle and the Honey-possum (all monotypic at the generic or familial level). Category 2 contained a frog and two birds (Ground Parrot and Noisy Scrub Bird). Relict species, however, also showed secondary adaptation and category 7 included several relict frogs and reptiles as well as recent avian and mammalian colonizers. Kikkawa *et al.* (1979) further point out some of the ecological features of the heathland habitat to which animals have had to adapt. They included low pH in the wetter sites, low soil nutrients, sandy or rocky substrate, restricted and special nature of food resources (such as nectar), low productivity, important role of fire, dense ground cover and high incidence of toxic substances in plant tissues.

This incisive review of the ecological, zoological, evolutionary and historical aspects of the fauna of this vegetation type could well be emulated for other vegetation types. Kikkawa *et al.* (1979) note that the sequence presented for heathlands has parallels in tropical and subtropical each major vegetation type in Australia, great progress would be made in understanding community ecology and evolution on the continent.

There have been a few other attempts at similar studies. Hutchings & Saenger (1987) review the vertebrate and invertebrate faunas of Australian mangrove vegetation.

Mangroves are not the primary habitat for most animals occupying them; many are casual visitors. Possible benefits to be derived from the use of mangroves include fewer predators and competitors in mangroves; abundant food (e.g. nectar) at critical times of the year; augmentation of the potential food supply of terrestrial predators by marine invertebrates; the presence of vascular plants with fleshy succulent leaves; and the abundance of detritus on the forest floor (Hutchings & Saenger, 1987).

Terrestrial vertebrates reported from mangroves include mammals, reptiles and especially birds. Over 200 species of the last group occur in mangroves, of which only 14 are restricted to this habitat and 12 others use it as primary habitat only over part of their range. Sixty additional species use mangroves regularly, either throughout the year or in particular seasons. As small as these numbers are in proportion to the total numbers of birds, they represent a much richer avian fauna than in mangroves in other parts of the world.

The greatest number of avian mangrove-specialists in Australia occurs in the floristically richer and structurally more diverse mangroves of the northern tropics, especially in northwestern Australia (Ford, 1982). The mangroves in that area have been more stable geologically than those on Cape York Peninsula where Pleistocene fluctuations in sea level periodically eliminated mangrove areas. The majority of birds endemic to mangroves evolved from rainforest-inhabiting species. As Australia progressively dried during the late Cainozoic, low-lying mangrove areas along the northwestern Australian coast probably served as refugia for the dwindling stocks of formerly widespread rainforest species. As the mangrove areas were patchy, there was a greater probability of isolation, leading to speciation. Along the eastern seaboard, large areas of rainforest and mangroves may have remained contiguous longer, allowing continual interchange between the two environments until recently and minimizing the development of mangrove specialists. Today, mangrove habitat is patchy throughout.

Reptiles and mammals are similar to birds in that only a small proportion of species is restricted to mangroves. Most use it as secondary habitat or as a seasonal refuge. There are more species in tropical than in temperate mangroves.

Less is known of the invertebrates, but most terrestrial arthropods of mangroves are not restricted to that habitat. No species of ants or spiders are known to be so, whereas a few species of dipterans and lepidopterans are.

Heathlands and mangroves are vegetation types that are now fragmented and not in very extensive tracts. More continuous and widespread kinds of vegetation may have a greater number of animal species restricted to them. Generalizations in this regard await further study.

Refugia

The cyclic fluctuation of Australian climate in the late Cainozoic, superimposed upon a generally increasing and spreading aridity, provided conditions under which refugia played an important role in the distribution and speciation of animals.

During the wetter phases of climatic fluctuation, plant communities characteristic of mesic sites would expand and wet-adapted species would flourish as their habitat increased in area. During the drier phases, however, as mesic vegetation shrank back to the moister parts of the continent and was replaced elsewhere by xeric vegetation, two scenarios are possible. In the first, the ranges of wet-adapted animals would contract into those regions that still maintained a favourable climate and habitat. As the once continuous habitat became fragmented into widely separated pockets, the animal species would be broken up into isolated populations. Alternatively, some species might progressively become adapted to aridity and be able to occupy the new and expanding drier habitats, thereby extending their ranges. In the former case, animals retreat into refugia containing their ancestral environments. In the latter, they adapt to new conditions and radiate into new habitats.

With the return of wetter conditions, the refugia would have expanded and coalesced with a comparable expansion of the ranges of wet-adapted animals and a retraction of the dry-adapted ones into drier central areas or dry refugia — or their adaptive radiation into the expanding wet environments.

The Australian palaeoclimate has undergone a number of such cycles, particularly in the Pleistocene. The isolation of populations leads to their genetic divergence and reproductive incompatibility. During the expansive phase, they may come into contact again, possibly to interact competitively, but perhaps to extend into each other's ranges. When the following contractive phase occurs, both may become split into isolated populations, with each again forming new species in an iterative process. Thus, the alternate expansion and contraction of aridity would favour the proliferation of species. Some isolates may become adapted to new suites of conditions during times of change, only to be isolated in different kinds of refugia at the next cycle (for example, semi-arid habitat). Together, these phenomena should contribute to rapid diversification of fauna.

Countering this trend is the extinction of species at the extremes of climatic cycles. If contraction is extreme, habitat fragments may become too small to support permanent breeding populations and certain species may be lost. In other cases, whole refugia may be extinguished, along with the fauna they contain.

The fact that refugia serve as centres of speciation in fluctuating environments provides a tool for studying the past history of particular taxa. The areas where many species have been generated are likely to be areas where repeated isolation and expansion of distributional ranges have occurred in the past. That is, refugia often are centres of origin and dispersal. Cogger & Heatwole (1981; 1984), Pianka (1981) and Kitching (1981) mapped isoclines of species densities for various

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taxa (Fig. 5.10) and identified geographical areas where there were many species (centres of speciation and dispersal) surrounded by areas of relatively few species where there had been adaptive radiation into the more extreme habitats surrounding the centre. Certain areas seem to have served as refugia and centres of speciation for a number of taxa. For some, like the pygopodid lizards, the focus was in southwestern Australia, for others it was located in the north. For some the centre corresponded to one of the zoogeographic subregions such as the Southwestern (pygopodids) or Timorian (varanids). Others, particularly those involving taxa of more recent arrival, were in Cape York. Various older groups (elapids, scincids, agamids) showed a number of foci, perhaps related to different waves of immigration, including radiation of the dry-adapted taxa in the Eyrean Subregion. Some, such as the diplodactyline geckos, had their centres primarily in the arid interior. Similar treatments have been carried out at the generic level as a means of suggesting the centres of origin and dispersal at a lower taxonomic level (Pianka, 1981) (Fig. 5.10).

Given that during Australian Cainozoic history the general trend superimposed over the fluctuating climatic cycles has been one of increasing aridity, wet-adapted species might be expected to become extinct more frequently than dry-adapted ones and that there would be less opportunity for secondary adaptation to wet conditions. Thus, the dry-adapted fauna would be favoured in the long run over the wet-adapted one. This topic is discussed further below in relation to faunal imbalances in various climatic zones.

Another prediction from the progressive drying of the Australian continent is that moist refugia would increasingly become more common than dry ones. That is, moist areas would be reduced in size during arid expansion more than would dry areas during the wetter periods. In this context it is important to consider the kinds of refugia that have been identified in Australia. As predicted, most consist of habitats that maintain moisture during relatively dry periods. In addition to the generally moister peripheral regions, mountain tops have served as refugia. As one goes up mountains conditions get progressively wetter. During generally moist conditions climate and vegetation favouring wet-adapted species are widespread and animal species may have extensive distributions along mountain ranges and perhaps even out onto slopes or plains. With expanding aridity, the moist climatic and vegetative zones move upward and become discontinuous until only isolated mountain tops provide favourable habitat (Archer, 1984e). Habitat and species ranges become fragmented in the classical sense of refugia. A change to wetter conditions would result in expansion of their ranges, perhaps to coalesce or overlap. Conversely, a change to drier conditions might mean their extinction on lower peaks or, in extreme cases, on all mountain tops. There is a number of examples among the amphibians (Tyler *et al.*, 1981), reptiles (Schuster, 1980) and invertebrates (Keast, 1981b) of isolated relicts in the mountain top refugia in the Great Dividing Range. Similarly, the peaks of the Stirling and Porongorup Ranges in Western Australia approach subalpine conditions and contain relict mygalomorph spiders (Main, 1981a).

River banks, gorges and gullies also serve as refugia. During dry periods conditions remain moister there than generally obtain elsewhere and some species may survive only in such limited habitats.

Secondary habitats may serve as refugia if the primary habitat becomes reduced or disappears altogether. The role of heathlands and mangroves as refugia for rainforest species during past arid pulses has already been discussed.

Wet habitats have a lower species diversity of birds than do drier ones (Brereton & Kikkawa, 1963; Kikkawa, 1974). Perhaps there was extinction of more wet-adapted species during arid expansions than of dry-adapted ones at any time. Birds from the wetter habitats had stronger associations of species, suggesting that they occur in discrete assemblages that have a real discontinuity with the more loosely structured assemblages from arid regions (Fig. 5.11; Kikkawa, 1974).

Although moist habitats have served most often as refugia, this has not been exclusively the case. For example, grass-wrens (*Amytornis*) are inhabitants of the arid zone where they occupy primarily *Triodia* habitats. Isolation of populations, leading to speciation, appears to have resulted at least in part from dissecting of *Triodia* habitat by invading savannah grassland, *i.e.* leaving the populations of grass-wrens in semi-arid refugia (Keast, 1958a).

In conclusion, refugia in Australia have more often been moist areas surrounded by aridity rather than the reverse. At the present time, mountain tops or other locally moist areas are serving as refugia for some species.

Barriers

Animals vary in the ease with which they can cross barriers; what may constitute a barrier for certain species may not hinder the movement of others. For this reason, geographic subregions based on one group may not be applicable to other taxa. Yet, as noted above, many taxa have similarities in distributional patterns that relate to physical and climatic features deemed to be barriers. There are certain features that commonly prevent or reduce the movement of many kinds of animals. Some of these have been mentioned briefly in connection with delimitation of the boundaries of zoogeographic subregions. They will be discussed in general terms now and applied later to the interpretation of speciation. Barriers may be physical, climatic or biotic.

Physical Barriers. For terrestrial animals, these include topographic features such as mountain ranges, steep rift valleys and bodies of water (Keast, 1981b). The sea, of course, is a major barrier to the movement of terrestrial animals and its role in the isolation of Australia during its northward drift has been discussed. The ability of animals to cross open sea water varies greatly. Obviously, flying animals such as birds, bats and insects generally are better able to cross sea barriers than are more sedentary species such as earthworms or frogs. The relative ineffectiveness of sea barriers for the former groups is evident from the many records of land birds found as solitary, "accidental" individuals on islands far afield from their usual range. At least four species of Australian birds are known to have reached and become established in New Zealand since 1830 and stragglers of others are common there and in various other Pacific islands (Keast, 1981a). Heatwole *et al.* (1981) record 18 species of Australian mainland birds reaching One Tree Island, Great Barrier Reef, over a five-year period. Migratory birds are the prime example of indifference to oceanic barriers; some species cross long stretches of sea water on an annual basis.

Many flying insects readily cross extensive sea water barriers, either by actually flying or by passive dispersal by wind currents. The number of species and individuals reaching remote islands in this way is astounding. Farrow (1984) found that at Willis Island in the Coral Sea at least 13 influxes of airborne insects from Queensland (minimum distance 450 km) and possibly one influx from New Guinea (minimum distance 600 km) occurred during winds from the mainland in less than one year. At least 51 species were involved. Heatwole *et al.* (1981) note that minimal rates at



Figure 5.10 Isocones of species density of some reptiles and butterflies in Australia. (After Cogger & Heatwole, 1981, Pianka, 1981; Kitching, 1981); a. Elapid snakes; b. Scincid lizards; c. Pygopodid lizards; d. Lizards of the genus *Varanus*; e. Lizards of the genus *Amphibolurus*; f. Papilionoid butterflies.

[L. Bridges]

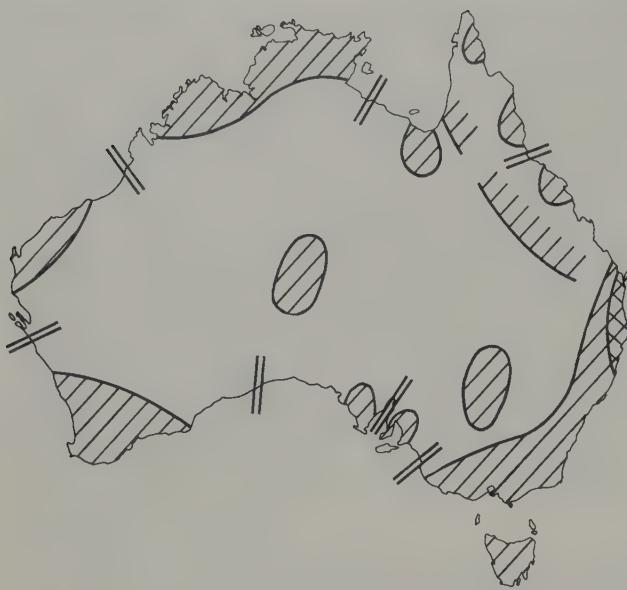


Figure 5.11 Refuges (hatched areas) and barriers (parallel lines) proposed to account for bird speciation in Australia. (After Horton, 1984)

which above-ground arthropods arrived on One Tree Island varied from 20 to more than 50 species per two-month period. Traps on ships and aircraft have revealed that even at great heights and over mid-ocean there are significant numbers of small arthropods of various kinds dispersing (Holzapfel & Harrell, 1968). Not all of these are flying forms. Some are young spiders floating on gossamer and others are minute forms, such as mites, that were probably blown upward by wind into the upper airstreams.

Some small animals take advantage of the volant powers of other animals and "hitch-hike". For example, snails may be transported in mud on birds' feet (Malone, 1965) and, of course, internal parasites and ectoparasites such as lice, ticks and fleas accompany their flying hosts.

Aerial transport is not the only method of crossing saltwater barriers. Sea currents themselves can be dispersal agents. Flotsam such as floating logs, coconuts or other terrestrial debris may harbour animals and transport them. This method is probably more frequent than is usually supposed. For example, Heatwole & Levins (1972) dissected 59 pieces of flotsam in the Caribbean and found that 25% of them contained at least one live terrestrial invertebrate and often there were many. Pseudoscorpions, snails, spiders, mites, millipedes, isopods, worms and 19 families of insects were represented. There is difficulty accounting for the presence of relatively large, flightless animals such as centipedes, spiders and lizards on remote islands other than by flotsam transport.

The ease with which a taxon crosses sea barriers by flotsam transport is dependent upon tolerances to the physical rigours of temperature, desiccation, salinity and food and water deprivation experienced during the voyage and whether special reproductive adaptations exist that improve chances of establishment once in a new location. An example of the latter is parthenogenesis, the ability of females to reproduce via unfertilized eggs and in the complete absence of males. Thus, a minimum of only one female individual, not a pair, has to survive the voyage.

Sea water barriers have been of significance in Australia in certain ways:

(1) Gondwana was not likely an unbroken land mass. The Antarctic part was probably an archipelago (Archer, 1984a). If so, Antarctic water gaps may have acted as a faunal filter, selectively permitting easy access to Australia by alien taxa that crossed such barriers easily, but denying access to other, less vagile forms. One may speculate that this explains why only the microbiotheriids among the ancient marsupial stock seem to have made the journey.

(2) Large epicontinental seas covered much of the central part of Australia in the early Cretaceous and separated the continent into a series of islands (Fig. 5.12), among which faunal exchange would have been reduced. This early separation may account for the distribution of some of the older faunal elements. For example, some spiders, the morabine grasshoppers and some of the geotrupine scarabs have distributional patterns centring on the larger of these Cretaceous islands (Main, 1981a; Howden, 1981). Speculatively, the barriers formed by those continental seas could explain the restriction of relicts like the chelid turtle *Pseudemydura umbrina* to southwestern Australia (Burbidge *et al.*, 1974) or the origin of pygopodid lizards in the southwest, when it was a Cretaceous island.

(3) During much of the Tertiary, the continent was isolated by oceans, a situation that has persisted to the present day.

(4) Marine incursions at various places along the periphery of Australia during the Tertiary (Fig. 5.13) may have served as barriers, fragmenting peripheral distributions. The most important one was in the Nullarbor from the Late Eocene to the Miocene (Nelson, 1981). Others were along the western coast and in the lower part of the Murray-Darling basin (Galloway & Kemp, 1981).

(5) Even after the Australian and Asian Plates collided, there were water gaps separating the emergent parts of those land masses. These acted as faunal filters, much as described above for the Antarctic archipelago. Bats and birds, for example, were more successful in colonizing Australia from Asia than were the non-volant placental mammals. The faunas of Australia's offshore islands are influenced today by the varying ability of different taxa to cross sea barriers.

(6) Alternate opening and closing of sea barriers between Australia and New Guinea in the north and Tasmania in the south has had an effect on faunal exchanges and speciation patterns.

In the late Tertiary and the Pleistocene, there were marked eustatic changes. During glacials, large portions of the world's supply of water were locked as ice on the polar caps and sea level dropped accordingly. Conversely, during interglacials when the caps melted, sea level rose again. Levels reached 200 m below current sea level and rose more than 40 m higher than at present (Galloway & Kemp, 1981). During periods of lowered sea level, when land connections between Australia, New Guinea and Tasmania existed, there could be interchange of fauna across Torres Strait and Bass Strait, limited only by whatever habitat barriers might have existed.

As sea level rose and the land connections were severed, followed by progressive widening of the water gap, faunal exchange would have diminished with the degree of reduction varying among taxa. At present, the proportion of New Guinean elements decreases and that of Australian ones increases in the Torres Strait's insular faunas from north to south (Cameron *et al.*, 1978).



Figure 5.12 Land and epicontinental areas of Australia in the Early Cretaceous. Present day coastlines in dashed lines. Cretaceous coastlines in solid lines. (After Howden, 1981) [L. Bridges]

Bodies of freshwater such as lakes and rivers can also serve as barriers for the less vagile terrestrial animals. Australia is one of the poorest continents in terms of bodies of freshwater and there are few present-day freshwater barriers of any significance. In the past, however, there were extensive freshwater systems that may have influenced animal distribution. A number of large inland lakes and marshes replaced the withdrawing Cretaceous marine seas and persisted for some time. These could have acted as barriers for terrestrial animals. Later, during moist Pleistocene periods (see below), freshwater lakes in the interior combined with mountain ranges would have formed barriers (Fig. 5.14) separating previously continuous ranges of widespread dry-adapted species (Kluge, 1967a).

Mountain ranges are effective barriers for some taxa. Australia is relatively flat and most mountain ranges are of limited geographic extent or are very low. There are, however, elevated segments and dissected plateaus in the central deserts, Arnhem Land, the Kimberleys and the southwestern corner (Keast, 1981b). The Great Dividing Range, with its altitudinal zonation of climate and vegetation, separates many taxa on an east-west basis and seemingly poses a barrier to faunal movement. The Flinders Ranges and the Hammersley Plateau may have been barriers to east-west and north-south movement, respectively (Fig. 5.14).

Climatic and Habitat Barriers. Allusion to climatic differences as barriers forming some of the boundaries of zoogeographic subregions has already been made.

An important consideration is the nature of previous climatic barriers in the Torres Strait region. An older view was that during Pleistocene glacials, when sea level was lowest and land connections broadest with New Guinea, the climate tended to be cool and moist. Conversely, interglacials with high sea level and severed land connections were believed to be relatively warm and dry (Horton, 1972). This view prompted the belief that wet-adapted fauna could easily cross land connections during glacials. More recent evidence suggests a different climatic pattern, with glacials being cool but dry and interglacials warm and moist (Bowler *et al.*, 1976; Flenley, 1979; Galloway & Kemp, 1981; Kershaw, 1981; Keast, 1981b). If so, then at times when climate was most conducive for transit, land connections would have been closed. When there were broad land connections, arid barriers would have prevented passage of the predominantly wet-adapted New Guinean species into Australia. Indeed, Kikkawa *et al.* (1981) show that the dry-adapted Australian taxa were able to colonize the dry savannah areas of southern New Guinea better than the New Guinean rainforest ones were able to colonize Australian rainforest on Cape York.

Neither of the above generalizations cover all cases. Then, as now, there were significant local and regional differences in climate and there were north-south shifts in climatic belts, such that at times the centre of aridity was further north than at others (Keast, 1981b). Nix & Kalma (1972) indicate that at 14,000 years ago, when sea-level was 120 m below present levels, the broad land connection between Australia and New Guinea was covered by xeric to sclerophyllous vegetation, with New Guinean rainforest contracted and re-



Figure 5.13 Marine incursions (black areas) onto the Australian continent in the Tertiary. (After Galloway & Kemp, 1981)

mote from similar habitat in Australia (Fig. 5.15). At 8,000 years ago, however, when sea level was 30 m below present level and a land connection with New Guinea still existed, though narrowed, the climate was wetter and New Guinean and Australian rainforests were in close proximity (Fig. 5.15). Clearly, there were at least some periods when sufficiently moist conditions prevailed during lowered sea level to permit migration of wet-adapted fauna from New Guinea into Australia. Such conditions probably did not occur in every glacial cycle. Horton (1984) estimates that three of the Pleistocene cycles would have been suitable.

Biotic Barriers. Several kinds of distributional patterns of one species relative to another have been recognized. Species that do not overlap in geographic range are said to be allopatric. A special case is when such species have mutually exclusive ranges, but which are contiguous along a broad zone. Such species are said to be parapatric. Where their geographic ranges broadly overlap, the species are said to be sympatric. If within the general region of overlap, species also occupy the same localities and habitats they are additionally considered to be syntopic.

A species of animal may pose a barrier to another species. Much has been made of interspecific competition as a determinant of distributional patterns. Closely related species often are allopatric or parapatric. Allopatry may result from the parent population being fragmented by some non-biotic barrier and the two isolated populations then diverging. Their spatial isolation is imposed by the non-biotic barrier, not by whether or not they are potential competitors. In the case of parapatric species, however, there is no physical separation and a common interpretation is that in one region one species has a competitive advantage and eliminates the other, the reverse being true elsewhere. Thus, if conditions change along an environmental gradient, the point where the competitive advantage shifts from one species to another is where the boundary between the two occurs, with each species competitively displacing its opposite number from its own range. Empirical demonstration of competitive exclusion is difficult and involves detailed ecological study. Often circumstantial evidence was accepted, circular reasoning employed, and competitive exclusion uncritically invoked as an explanation of parapatric distributional patterns. As a result,

this answer has become suspect even though very careful, detailed studies unequivocally have demonstrated competition to be operative in some instances. The role of competition is one of the most hotly debated of current ecological issues. The best that can be concluded at the moment is that competition can be a very important zoogeographic factor and that parapatric distributions are suggestive of it, but warrant closer examination and assessment of alternative explanations in individual cases.

Less attention has been paid to the zoogeographic role of competition between species that are not closely related. Even phylogenetically distant taxa, however, may share similar requirements and compete with each other for resources. For example, some birds, bees and hawkmoths compete for nectar (Carpenter, 1979). Seed-gathering ants and granivorous rodents show reciprocal abundances in some desert habitats and experimental manipulation of populations has demonstrated a competitive interaction (Brown *et al.*, 1979). The extent to which such taxa limit geographic ranges of others through competition is a field that remains to be explored.

Biotic interactions other than competition also may be important. For example, interspecific aggression, territoriality, intense predation, disease or parasitism theoretically could eliminate a species from an area and limit its range. These interactions, like competition, require detailed ecological study.

Corridors, Dispersal Routes And Points Of Entry

Corridors are the opposite of barriers. They permit rather than block movement. They are narrow regions of favourable habitat extending into an otherwise harsh environment. Often corridors connect two parts of an animal's range and permit migration between areas. They can take different forms, such as a narrow land connection across bodies of water (sometimes called land bridges), narrow bands of favourable habitat along river banks, the floors of valleys or gorges or merely bands of vegetation related to local peculiarities of

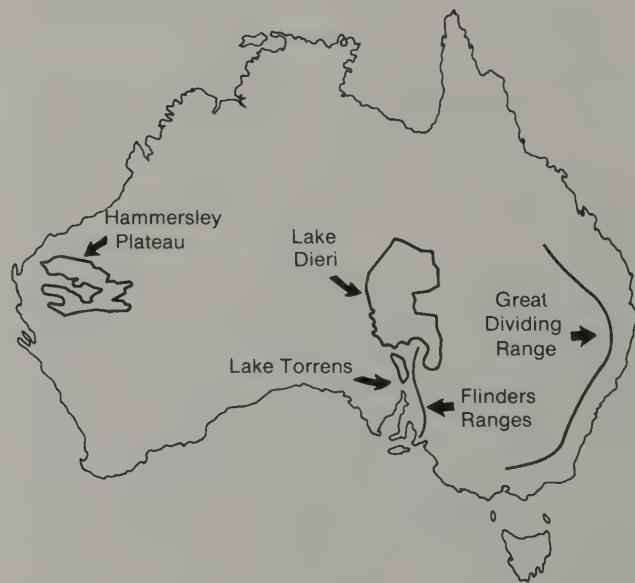


Figure 5.14 Principal physical barriers for xeric animals during Pleistocene wet periods. (After Heatwole, 1976) [L. Bridges]

5. TERRESTRIAL COMPONENTS AND DISTRIBUTION

soil, topography or climate. Like barriers, corridors may not be permanent, but may be broken and reformed with changing climate. They may affect speciation patterns in two ways:

- 1) they may reduce isolation by facilitating faunal exchange between otherwise isolated areas and in this way inhibit speciation;
- 2) conversely, they may promote speciation by allowing passage of taxa to otherwise inaccessible areas which are then isolated when the corridor is broken.

Corridors probably have played a significant role in speciation in the Eyrean Subregion. The central deserts seem relatively uniform in topography and few physical barriers are evident. Yet, the distributional patterns of animals indicate that there has been considerable isolation. Isolation may arise from differences in substrate and vegetation. Pianka (1981) identifies three major different habitat types: sandplains, sandridges and mulga. These are interdigitated in complex ways and although there are species that span two or more of them, there are others that are restricted to particular ones. Pianka postulates that shifting of habitat boundaries and the opening and closing of corridors between fragmented areas of similar habitat account for the recurrent cycles of isolation followed by movement to new areas which is requisite for proliferation of species. He identifies a number of corridors in central Australia (Fig. 5.16). Similarly, Keast (1958a) postulates a corridor of desert "spinifex" (*Triodia*) from the arid centre to the base of the Gulf of Carpentaria during periods of climatic deterioration to explain the close relationship between two geographically distinct species of grass-wrens.

Dispersal routes may be ecological corridors or isthmuses which have contributed to the movement of species from one region to another. On a longer-term basis, dispersal routes may reflect the gradual movement of a higher-level taxon outward from its centre of origin through different types of habitat, not by following corridors of the original habitat, but

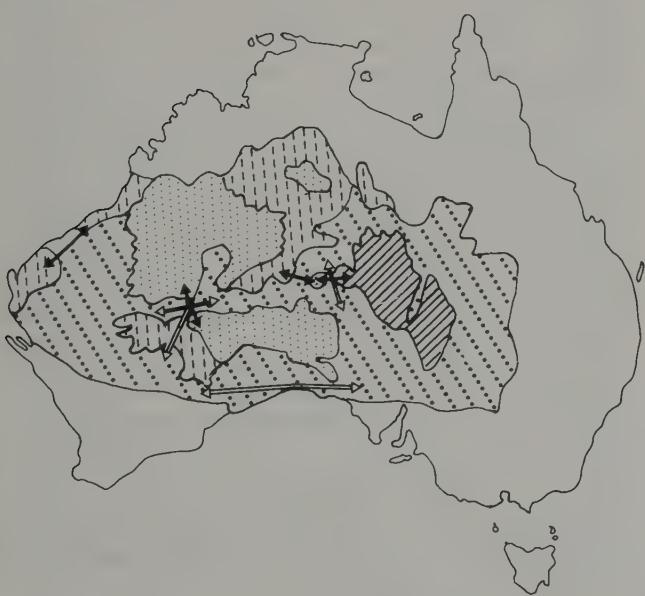


Figure 5.15 The major arid habitats and dispersal corridors of Australia. Arrows indicate probable location of corridors between regions of sandy habitat (black) or mulga habitats (white) arising from Quaternary habitat shifts in areas of interdigitation. Finely stippled areas represent sandplains, coarsely stippled areas (two types) represent sandridges, and hatched areas represent mulga habitat. (After Pianka, 1981)

[H. Hunt]

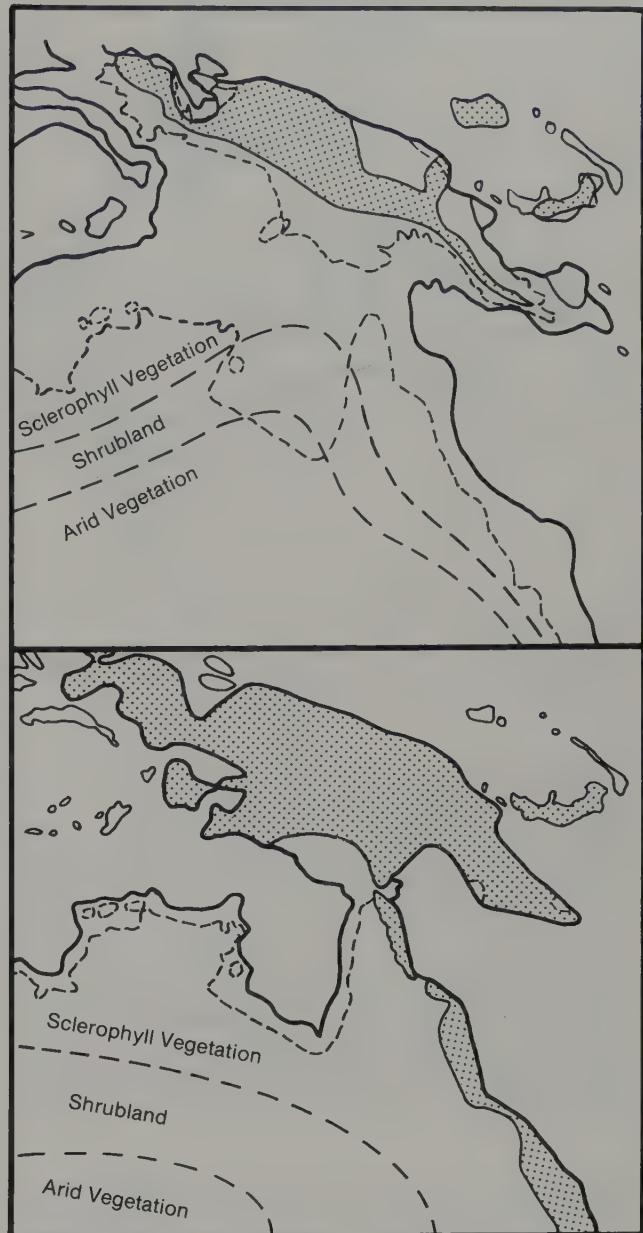


Figure 5.16 Vegetation of the land connection between Australia and New Guinea at two different times in the Quaternary. Upper: sea level at 120 m below present level, about 14,000 years ago. Lower: sea level at 30 m below the present level, about 8,000 years ago. Rainforest is stippled. Short-dashed lines represent present coastlines; solid lines paleocoastlines; long-dashed lines approximate limits of vegetation types. (After Kikkawa *et al.*, 1981) [L. Bridges]

by adaptive radiation into new kinds of habitat, that is, by crossing barriers through adapting to the environments of the barrier. Species density maps again are useful in identifying such dispersal routes. The highest species densities are in the centre of dispersal with declining numbers outward along the route of dispersal. Figure 5.17 shows those identified by Cogger & Heatwole (1981; 1984) as important to reptiles. They probably are applicable to other taxa as well, e.g. birds (Serventy & Whittell, 1976).

Of particular significance are the patterns of geographic distribution and species density that identify the point of entry of a taxon into Australia. Taxa that have been resident for long periods (the old Gondwanan Elements and the earliest of the Tertiary Asian Elements) may have radiated from one



Figure 5.17 The major dispersal routes postulated for Australian reptiles. (After Cogger & Heatwole, 1981)

or more secondary centres leading to patterns that may obscure the original entry point or centre of origin. For later arrivals without secondary centres of speciation and dispersal, however, present day distributions may indicate the route whereby they entered Australia. Many of the modern arrivals are found only on the tip of Cape York and are closely related to Papuan species. Clearly, the point of entry of such species into Australia is Cape York and the source was Papua. There are other taxa that have most of their species in northwestern Australia and their closest non-Australian relatives are in Timor or other Indonesian islands. Again, both the source and point of entry are obvious. These are the two most common recent points of entry into Australia from the north.

The prevalence of Cape York as a point of entry is probably related to several factors, including its close proximity to New Guinea, its frequent land connections with that land mass during Pleistocene glacials and the presence of "stepping stone" islands in the Torres Strait. Indeed, for many terrestrial taxa the Torres Strait has not constituted a serious barrier; rather, ecological differences between areas on either side have been of critical importance (Kikkawa *et al.*, 1981).

In this regard, the faunal patterns of the islands in Torres Strait are of importance. The western islands are extensions of the Great Dividing Range of Australia and are of Carboniferous igneous rock. In contrast, the eastern islands are of Pleistocene volcanic origin (Jennings, 1972) and are more similar to New Guinean than to Australian habitats. Scattered throughout are coral cays which originated from local reefs. The herpetofauna of the western islands has greater affinities with Australia, whereas that of the eastern ones is allied more closely to the New Guinean fauna (Cogger & Heatwole, 1981; Cogger & Heatwole, in prep.). The fauna of the coral cays contain mainly elements of the widely dispersed Indo-Pacific atoll fauna. This mixture indicates three dispersal routes: one from Australia toward New Guinea via the western islands, another from New Guinea toward Australia via the eastern islands and "sweepstakes" dispersal throughout the area. In each case, the distributions and routes of movement reflect the availability of appropriate habitat.

Given that the tip of Cape York is a common point of entry for taxa of New Guinean origin, Cape York, not surprisingly, is an important southward dispersal route for immigrants. Kikkawa *et al.* (1981) review the zoogeographical importance of Cape York for insects and terrestrial vertebrates. The most important of their findings can be summarized as follows: (1) the Cape, although a region of important faunal exchange, has been a filter varying in effectiveness according to the adaptations and habitat specializations of the taxa concerned; (2) southward dispersal of New Guinean rainforest forms was impeded partly because rainforests on the cape are disjunct (separated by drier barriers) with the larger and older isolates towards the south; (3) colonization rates have varied with climatic fluctuation; (4) faunal attenuation in both directions is marked (Fig. 5.18), but because of the mosaic of dry habitats and rainforest, is the result of interdigitation as well as intergradation; (5) for the least vagile group (frogs) only one species colonized and survived in the Australian post-Pleistocene rainforest while for birds, which are more vagile, 14 species established themselves in the northern part of the Cape in addition to those that expanded their range southward and speciated since colonization. New Guinean butterflies frequently colonize localities in Cape York and persist for a few years without becoming permanently established.

Speciation In The Pleistocene

The Pleistocene was a time of enormous change in a variety of the categories discussed above (Keast, 1981b). There were drastic changes in climate with accompanying expansion and contraction of the arid zone and alternating fragmentation and coalescence of peripheral refugia. Sea level lowered and raised, forming and breaking land connections. The scene is one of shifting barriers, boundaries and corridors and of repeated cycles of isolation and renewed contact of populations. These are conditions which favour accelerated rates of speciation.

Whereas divergence at the higher categories probably reflect events from the Tertiary back into extreme antiquity, many modern species and perhaps even genera, may have had their origin in Pleistocene times.

Horton (1984) incorporates climatic and sea level changes and physical barriers into a dynamic model of speciation (Fig. 5.19). A slight expansion and modification of it includes the following stages: (1) migration of a New Guinean ancestral stock into Australia during a suitable climatic period when sea level was lowered (Fig. 5.19a); (2) severing of the land connection and expansion of range southward from Cape York during a moist part of the cycle, separately on the two sides of the Great Dividing Range (Fig. 5.19b); (3) isolation of populations by expanding aridity, assisted by topographic barriers imposed by the Great Dividing Range (Fig. 5.19c); (4) during a second wet phase, the southern coastal species followed a moist, southern corridor into southwestern Australia and, when sea levels were lowered appropriately, into Tasmania (there to be isolated by the next severance of land connections); the species on the drier inland side of the Great Dividing Range followed the drier edge of the corridor into southwestern Australia; the northern isolate expanded southward on both sides of the Great Dividing Range and across a moist northern corridor into northwestern Australia (Fig. 5.19d); (5) a second arid expansion reformed the previous aridity barriers and isolated populations in each of the two northern corners of the continent, two in each of the southern corners, one on either side of the Great Dividing Range in the east and one in Tasmania (Fig. 5.19e). Each of these could form a species, and thus, just from this single sequence of events nine species (counting the New Guinean one) could be generated. During these changes, however, a second speciation cycle could begin by another

invasion from New Guinea during low sea-level. Superimposed cycles are not shown in Fig. 5.19 in order to prevent confusion.

Successive speciation cycles, like the above, could lead to a concentric pattern of species distributions. The more inland population would be the most dry-adapted (Fig. 5.19) and in wet periods would move further inland, following its drier habitat, to be replaced on the periphery by wet-adapted species. Several species cycles would generate a sequence of east-west pairs of increasing age and dry-adaptedness from the coast toward the inland. Eventually, the most dry-adapted ones might be spread widely in the centre to form an Eyrean distribution. The range of such species could be fragmented by watercourses during wet periods (Fig. 5.14) or by shifts in habitat boundaries.

Horton (1984) bases his model on the skink genus *Egernia*, but it probably has wider applicability as similar distributional patterns occur in such diverse groups as lizards, tabanid flies, birds and plants (Keast, 1981b). Clearly, events would not proceed exactly the same for all taxa. There would be differences in timing, in dispersal rate and sensitivity to moisture. Some isolates might become extinct, thereby eliminating part of the sequence. One would predict, however, that speciation patterns of a variety of taxa of New Guinean origin could be interpreted in this framework.

The timing of such events is not indisputable. Horton (1984) and many other zoogeographers consider them as Pleistocene; they may have been. There were, however, climatic fluctuations and land connections between Australia and New Guinea before the Pleistocene (Doutch, 1972). The possibility exists that Horton's (1984) sequence of events may be correct, but that they occurred earlier than he proposes.

Speciation, regardless of when it occurs, is dependent not only on changes in climate, vegetation and sea level, but upon certain attributes of the organisms themselves. Especially important are vagility, habitat selection and reproductive system. Keast's (1958b) demonstration of this phenomenon in the Australian chats is a good example. *Epthianura crocea*, the Yellow Chat, is sedentary and is found in marshy habitats of several widely separated river systems. Its specialized habitat and lack of movement means that the population in each river system has diverged as a distinct morphological isolate (incipient species) with the potential for producing a new species as long as conditions do not change and cause a coalescence of presently isolated habitats. At the other extreme, *E. tricolor* (the Crimson Chat) inhabits inland plains and savannahs (over a large, relatively continuous area), but shows no regional morphological divergence. This species exhibits nomadism and seasonal movements as an adaptive response to dry, unpredictable environments. Movements are continent-wide and multi-directional and serve to mix individuals from different localities. There are no regular breeding areas or times; the species is opportunistic in these regards. Unless pair bonds are maintained during non-breeding periods or the same ones re-established whenever and wherever conditions again are favourable, such opportunistic breeding would contribute further to mixing of individuals from different geographic origins. The above life history traits probably account for the fact that *E. crocea* is beginning to differentiate into morphological isolates and *E. tricolor* is not. Other species of chats are intermediate.

ACCOUNT BY TAXA

In the above Sections, the role of refugia, barriers, corridors, biotic interaction, present and past climate and vegetation were assessed in terms of their effect on animal distributions and speciation. Although examples have been supplied for each of these as appropriate, no overall assessment of how

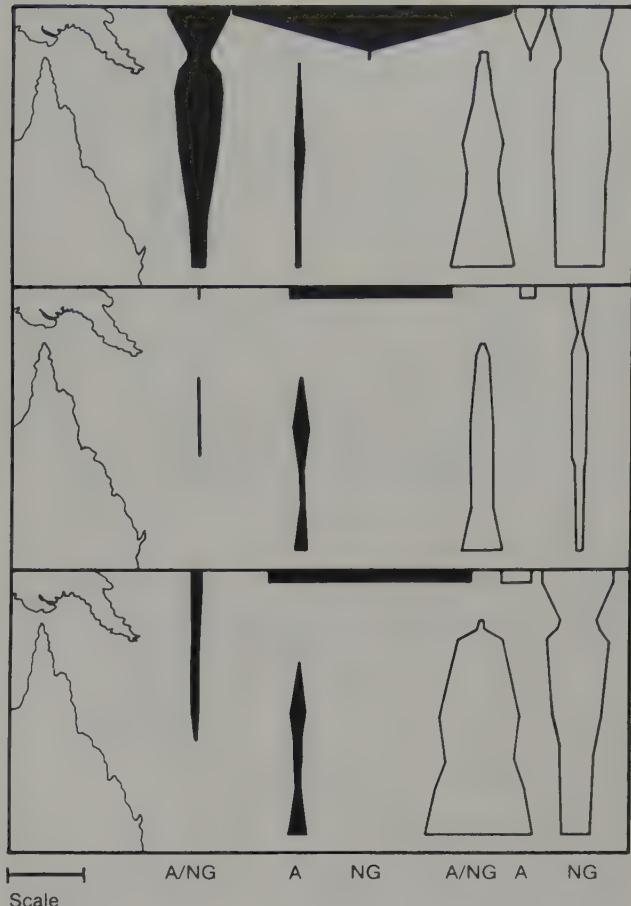


Figure 5.18 Diagrammatic representation of the transition in species richness from New Guinea to northeastern Australia of different components of the butterfly (upper), frog (centre) and reptilian (lower) faunas; A = Australian endemic species; NG = New Guinean endemic species; A/NG = species shared between Australian and New Guinea; black figures are rainforest species; white figures are open forest [L. Bridges]

particular taxa have responded to the totality of their environment was made. In this Section, a general synopsis of the major taxa of Australian animals and the factors believed to have influenced their evolution and distribution are presented. Not all instances of the way palaeoclimates and changes in barriers have affected distributional patterns can be given in a brief review such as the present one and to do so in detail would usurp much of the content of the volumes to follow.

Mammals

The native, terrestrial mammals are of three groups. The marsupials and monotremes collectively account for about 56% of the species, rodents for about 22% and bats for the remaining 22% (Baverstock, 1984).

The monotremes occur in Australia and New Guinea today and are known as fossils only from Australia as forms that resemble the Platypus more than the Echidna (Archer, 1981; Augee, 1984; Murray, 1984).



Figure 5.19 Postulated sequence of events in the immigration, dispersal and speciation of Australian terrestrial animals originating in New Guinea. Outer narrow line indicates boundary of land masses when sea level was low and New Guinea and Tasmania were connected to Australia. Parallel lines indicate barriers to dispersal. Different symbols indicate populations at different stages of divergence. For further explanation, see text. (After Heatwole, 1976)

A recent find of a fossil one from the Early Cretaceous (Archer *et al.*, 1985) is the oldest mammalian fossil from Australia and indicates that monotremes were in Australia well before separation from the rest of Gondwana.

Various views on the origins, phylogeny and migrations of marsupials have been expressed (see reviews by Archer, 1981; Archer 1984b; Kirsch, 1984).

The account by Archer (1984c) is the most comprehensive and evaluative one available and is the basis of the following summary. Marsupials originated in the Cretaceous, either in North America or South America. A diverse radiation in South America produced an array of different forms that invaded many niches and adopted different life styles. Among these were the microbiotheriids, the only South American group of marsupials belonging directly to the lineage giving rise to all known fossil and living Australian marsupials. Microbiotheriids probably dispersed southward into Antarctica and then to Australia in the Late Cretaceous or early Tertiary times, where they radiated into a great diversity of animals rivalling that of placental mammals in other continents and showing a number of convergences (sometimes previously mistaken for evidence of relationship) with the South American radiation. Among the extinct and living Australian forms are the equivalents of placental lions, cats, tapirs, rodents, wolves, marmots, moles, flying squirrels, as well as many types not directly comparable with any non-marsupial. The extinct species included giant, spectacular beasts, some of which lasted up through the Pleistocene and were contemporaries of Aboriginal man.

The microbiotheriid diversification probably began in Antarctica-Australia prior to the separation of Australia, with establishment soon thereafter of the three major Australian lineages: the Dasyuroidea, the Perameloidea and the Diprotodontia (Archer, 1984c).

The dasyuroids comprise three living (or recently extinct) families of 42 carnivorous or insectivorous species. The family Dasyuridae includes the genera of small mouse-like, rat-like or possum-like marsupials known as antechinuses (*Antechinus*, *Parantechinus*, *Pseudantechinus*), phascogales (*Phascogale*), dunnarts (*Sminthopsis*), planigales (*Planigale*), mulgaras (*Dasyurus*), kowaris (*Dasyurodes*), ningauis (*Ningaui*) and kulttarrs (*Antechinomys*), as well as medium sized quolls or native cats (*Dasyurus*) and the larger Tasmanian Devil (*Sarcophilus harrisii*) (Strahan, 1983). The other two families have only one species each. The Myrmecobiidae, represented only by the Numbat (*Myrmecobius fasciatus*) is now restricted to southwestern Australia and is endangered. The Thylacine or Tasmanian Wolf (*Thylacinus cynocephalus*) probably became extinct in the 1930's (see Chapter 20). It had become restricted to Tasmania, possibly eliminated on the Australian mainland by the Dingo.

The omnivorous Perameloidea include the bandicoots (Peramelidae, four genera and nine species) and the bilbies (Thylacomyidae, one genus, two species).

The herbivorous Diprotodontia has the greatest richness of living species (75), the most diversity of form and habit of any of the Australian marsupials and includes most of the spectacular, now extinct forms. There are three main lineages of living ones, (1) the Vombatoidea which includes wombats (Vombatidae, two genera, three species) and the Koala (Phascolarctidae, *Phascolarctos cinereus*), (2) the Phalangeroidea (possums) which includes the ringtails and large gliders (Petauridae, five genera, 11 species), the brushtails and cuscuses (Phalangeridae, three genera, six species) and the pygmy possums and feathertail gliders (Burramyidae, three genera, six species) and (3) the Macropodoidea which contains the potoroos, bettongs and rat-kangaroos (Potoroidae, five genera, nine species) and the kangaroos and wallabies (Macropodidae, nine genera, 39 species).

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There are two groups which have not been included in the above scheme because their relationships to other marsupials are problematical. One is the monotypic family Tarsipedidae (the Honey-possum, *Tarsipes rostratus*); it may belong to the Phalangeroidea (Archer, 1984c; see Chapter 33, this Volume). The other are the marsupial moles (*Notoryctes*) of the family Notoryctidae. They have become so morphologically specialized as burrowing animals that phylogenetic relationships are not clear.

This amazing marsupial radiation has produced, probably from a single microbiotheriid stock, nearly the entire gamut of mammalian types known, including arboreal, terrestrial and burrowing forms. They have become adapted to stark desert, tropical rainforest and cold alpine heath and all environments in between. There are carnivores, insectivores, omnivores, herbivores and nectar feeders. They hop, run, climb and glide. The adaptive radiation of the Australian marsupials is one of the most fascinating chapters in the book of evolution.

The fossil record in Australia is inadequate to indicate whether placental mammals of Gondwanan age ever existed in Australia. If they did, they became extinct. None of the modern Australian placental fauna belongs to the old Gondwanan Element.

Australia's native terrestrial placental mammals are only of three groups, rodents of the family Muridae, bats and humans.

The rodents originated in Asia, probably in the Miocene (about 25 mybp) and dispersed southward, probably first reaching Australia only in the Pliocene (four to five mybp) (Hand, 1984). Divergence at the subfamilial and tribal level probably took place outside the region with entry into Australia by different stocks taking place in three different waves.

The tribe Conilurini contains eight genera and 40 species of hopping mice (*Notomys*), tree-rats (*Conilurus*), rabbit-rats (*Mesembriomys*), stick-nest rats (*Leporillus*), rock rats (*Zygomys*) and some other rat-like taxa (Baverstock, 1984). They have diversified primarily in the semi-arid regions. There are two distantly related species of water rats (tribe Hydromyini). One (*Hydromys chrysogaster*) occurs in waterways throughout Australia and the other (*Xeromys myoides*) usually is found in mangroves. The genera *Uromys* and *Melomys* (tribe Uromyini) are tropical to subtropical rats occurring in forests and grasslands in the north; they are closely related to New Guinean taxa. Finally, the true rats (genus *Rattus*; subfamily Murinae) occur throughout Australia, but with the greatest species richness in coastal Queensland.

Both suborders of bats are well represented in Australia (Hall, 1984). The Megachiroptera or fruit bats are represented by one family (Pteropodidae) with five genera and eight species. They feed on fruit and/or nectar. Generally, they are confined to the northern and eastern parts of the continent. The Microchiroptera includes the insect-eating bats and are represented in Australia by five families, 16 genera and 51 species. Bats evolved from a small nocturnal insectivore in the Late Cretaceous or Early Eocene. Their early radiation occurred in the Old World and they entered Australia from the north prior to the Miocene (Hall, 1984). They are most abundant in the north; 57% of all Australian species occur on Cape York with decreasing numbers southward (17% in Tasmania). The eastern coast has a greater species density than other parts of the continent at equivalent latitudes. Availability of roosts seems to be one of the important local factors influencing distribution.

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Humans reached Australia and became established as part of the native fauna certainly more than 30,000 years ago as evidenced by fossil remains. Some estimates would place it as much as 120,000 years ago (Archer & Aplin, 1984). There probably was more than one early entry.

Birds

Some birds cross water gaps relatively easily and hence Australia was never so isolated from them as it was from many other taxa. As a result, the origin and time of arrival of some groups of birds in Australia is shrouded in mystery (Keast, 1981a; 1984). There are some groups, however, whose history is less in doubt. Some of the higher taxa, such as the ratites (emus and cassowaries), penguins, megapodes and parrots are almost certainly of Gondwanan origin. The kingfishers (Alcedinidae) have been in Australia a long time and have undergone extensive radiation within the continent and produced some distinctive endemics. Whether they were present prior to separation of Australia from Antarctica or were merely an early group to cross the still extensive water gap during northward movement cannot be ascertained from available data.

In contrast to previous views (Keast, 1981a; 1984), more recent evidence from Sibley & Ahlquist (1985) indicates that the Australian oscine passerine birds are in two major groups, each with a different history. The Corvi (three superfamilies and ten families in Australia and New Guinea, including the lyrebirds, Menuridae, and scrub-birds, Atrichornithidae, in the classification of Sibley & Ahlquist) is an old group which began its radiation 55 to 60 mybp, i.e., while Australia was still connected to Antarctica. It probably originated in that part of Gondwana that is now Australia rather than having diverged from a South American group. The other oscine group (Muscicapidae) originated either in Africa or Asia. As Australia approached Asia during the Tertiary, two types of movement occurred. Members of the Corvi dispersed from Australia to Asia and radiated there and in other parts of the world; members of the Muscipapidae colonized Australia from Asia. The suboscines, as redefined by Sibley & Ahlquist (1985), are represented in Australia only by the pittas (Pittidae) which are recent arrivals from the north.

Reptiles

Among the extant reptiles of Australia, none is of certain Pangaean origin. The ancient and diverse reptilian fauna included dinosaurs of various types as well as a wide variety of other forms. These groups became extinct without leaving any derivative modern forms.

One of the curious features of the history of reptiles in Australia is that the most diverse and successful modern taxon, the Lacertilia, may have originated in Australia in Pangaean times. There are fossils of the very earliest lizards from the lower Triassic of Australia (Molnar, 1983b; 1984a). Estes (1983) postulates Australia to have participated in a Pangaean origin for the modern families Gekkonidae, Agamidae and Scincidae. One view is that many of the present day representatives of these families in Australia can trace a continuous lineage there from Pangaean times. All three families have radiated extensively in Australia. The more common view, however, is that except for the geckos, these lizards thrived and radiated elsewhere in the world, but disappeared from Australia until their re-invasion upon contact of the Australian and Asian Plates millions of years later (Tyler, 1979a; Heatwole & Taylor, in press). Although a firm

decision on this matter cannot be made because of the incompleteness of the fossil record in Australia, the latter view is the one tentatively followed in this Chapter.

The turtle family Chelidae (side-necked tortoises) is certainly a Gondwanan taxon. The only places other than Australia in which it occurs is South America and New Guinea. By contrast, other families of turtles (except sea turtles and one recent immigrant from New Guinea, see below) are now absent from Australia.

The gekkonid subfamily Diplodactylinae is another likely reptilian candidate for a Gondwanan origin (Tyler, 1979a). It has radiated extensively in Australia. The suggestion by Kluge (1967b) that diplodactylines had a southwestern Asian origin no longer seems tenable (Tyler, 1979a). The family Pygopodidae (scaly-foots) is derived from geckos within Australia and attests to the antiquity of the gekkonid lineage there.

Most Australian reptiles probably belong to the Asian Tertiary Element. Many have radiated extensively and were probably among the first groups to enter the continent as it approached the Asian Plate.

The skinks are diverse and have the largest number of species in Australia (nearly 300) of any reptilian family. They have radiated into a variety of arid and mesic habitats and obviously have a long history on the continent. Cogger & Heatwole (1981; 1984) consider that they probably arrived on a number of occasions and that separate histories would have to be traced for different subfamilies or even genera, before their history could be understood fully. That task is hampered by an imperfect knowledge of their taxonomy.

The successive invasions of varanids and agamids already have been discussed. Most of them probably first entered in the Tertiary, but a few invasions may have occurred in the Pleistocene.

The terrestrial Elapidae (front-fanged venomous snakes) probably originated in Asia and reached Australia when more primitive colubrids (their ancestors) were waning in Asia and before the modern colubrid radiation began (Cogger & Heatwole, 1981). They show extensive radiation in Australia and are the dominant family of snakes. The Typhlopidae (blind snakes) and Boidae (pythons) have radiated in Australia, presumably from ancestors arriving from Asia in the Tertiary.

The geckos of the subfamily Gekkoninae are pantropical and are remarkable for their powers of transoceanic dispersal. They probably entered Australia several different times and their origins are obscure. Some of them, like the genera *Heteronotia* and *Phyllodactylus*, have speciated in Australia and probably arrived in the Pleistocene or perhaps Tertiary. Species of the genera *Cyrtodactylus*, *Hemidactylus* and *Lepidodactylus* are not restricted to Australia, but are widespread on islands, beaches and strands. They probably invaded repeatedly from a variety of sources, up to the present time (Cogger & Heatwole, 1981).

By the Pleistocene, many modern genera of Australian reptiles were present and even a number of extant species were represented as fossils (see review by Heatwole & Taylor, in press). These genera had become widespread in Australia and had undergone a certain amount of adaptive radiation. Speciation and further adaptive radiation within Australia was influenced greatly by Pleistocene events (see below), but few new, higher taxa made their appearance in Australia after the Tertiary. The Quaternary was short in comparison to the Tertiary and the rate of immigration per unit time may not have changed. Alternatively, most niches may have become filled or the pool of potential dispersers had become exhausted.

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A probable Pleistocene entry has been postulated for the *indicus* group of varanids (goannas), the gekkonine geckos, the Pitted-shelled Turtle *Carettochelys*, the agamids *Gonocephalus* spp. and *Physignathus lesuerii* and the terrestrial colubrid snakes (Cogger & Heatwole, 1981). The latter group is worldwide in distribution and has radiated extensively in all continents but Australia. They account for most of the species of snakes in the world. Yet, only three terrestrial genera (containing five species) occur in Australia. Cogger & Heatwole (1981; 1984) suggest that they probably arrived late in New Guinea and entered Australia from there during a Pleistocene regression of Torres Strait or by fortuitous seawater dispersal.

A note of caution regarding the above interpretation of reptilian history should be sounded. Although the consensus view (and that of the author) is reported in this account, there are some that would consider certain elements, indicated as Asian Tertiary ones in this Chapter, to be Gondwanan. For example, Schuster (1980) suggests a Cretaceous, Gondwanan age for some scincid lineages in Australia. Witten (pers. comm.) considers some of the Australian agamids as part of the Gondwanan Element. An open mind should be maintained regarding the age of some of the more extensive of the reptilian adaptive radiations; they may be older than currently believed.

Frogs

Ancient amphibians or labyrinthodonts were present in Australia and reached their greatest diversity there in the early Triassic (Warren, 1983). They subsequently became extinct worldwide, are not known in Australia after the Early Jurassic (before the fragmentation of Gondwana) and have no significance for the modern Australian amphibian fauna.

All modern Australian amphibians are anurans (frogs), most of which are clearly of Gondwanan origin (Tyler *et al.*, 1981). Although there are no frog fossils from Australia prior to the mid-Miocene (Tyler, 1983), the combined circumstantial evidence of South American affinities and extensive adaptive radiation into many habitats throughout Australia, indicate a Gondwanan origin for the two major families, the Hylidae and the Myobatrachidae (Tyler, 1979a; White, 1984), which account for 94% of the total frog species of Australia.

Speciation within these old families has been traditionally interpreted along the same lines as Horton's (1984) model, discussed above. That is, expanding and contracting aridity and rising and lowering sea levels in the Pleistocene alternately isolated populations in southwestern Australia and Tasmania and permitted their expansion and reinvasion. Speciation was postulated to have occurred during periods of isolation. Series of sibling species of different degrees of affinity with southeastern taxa were considered to represent sequential episodes of immigration and isolation. This pattern seems to occur in various taxa of Gondwanan origin (Main *et al.*, 1958; Littlejohn, 1961; 1981; Watson & Littlejohn, 1985). It corresponds closely with known Pleistocene events. Migration is viewed as having taken place primarily from southeastern Australia into southwestern Australia during moist periods, with much less movement in the reverse direction. Some movement is postulated in both directions between southeastern Australia and Tasmania during sea level lowering (Watson & Littlejohn, 1985).

Some of these interpretations are contested by Roberts & Maxson (1985) on the basis of immunological and electrophoretic studies. They suggest *in situ* speciation in southwestern Australian frogs rather than multiple invasion from the east. The taxa studied were *Crinia* and *Heleioporus*, genera previously viewed as providing support for the multiple invasion hypothesis.

The research of Robert & Maxson (1985) also calls into question the timing of the separation of southeastern and southwestern taxa. Whereas the multiple invasion hypothesis places it as occurring in the Pleistocene, Roberts & Maxson suggest, on the basis of molecular clocks, that it took place in the Tertiary. That molecular clocks keep constant time and run at the same speed in all organisms seems to be an article of faith among the devotees of this approach, but is disputed by some biochemists (Tamiya, pers. comm.). The multiple invasion hypothesis, however, does not provide an adequate explanation of frog speciation in southwestern Australia and the timing of separation of eastern and western frog faunas must be reconsidered carefully.

Essentially, the controversy is whether the biogeography and speciation of these frogs conforms to a Pleistocene dispersal model or to a Tertiary vicariance one. Regarding these two explanations as mutually exclusive alternatives, however, restricts heuristic thinking. Observed biogeographic patterns likely arose as a result of vicariant processes in combination with dispersal. The task is to separate the relative importance of the two. Two separate aspects of the problem must be distinguished. The timing is a different problem from that of whether dispersal or vicariance played a major role. Linking these two aspects may lead to unrealistic polarization in interpretation.

In light of the above, a reassessment of the origins of Tasmanian frogs and other groups, such as lizards, may be warranted. Does the older taxon (frogs) display a Tertiary separation with *in situ* speciation patterns that superficially track Pleistocene events? Has the more recently arrived taxon (lizards) actually undergone speciation in the Pleistocene? Or, do Australian lizards parallel the situation proposed by Roberts & Maxson (1985) for frogs and have they an earlier arrival time in Australia than usually postulated? Clearly more research is required. The biogeography and speciation of Australian hylid and myobatrachid frogs will be an important part of that research.

In contrast to the Gondwanan families Hylidae and Myobatrachidae, the Microhylidae is part of the Tertiary Asian Element. This family is widespread throughout the world, but poorly represented in Australia (two genera with eight species, all on Cape York Peninsula or in Arnhem Land). Tyler (1979a) suggests that they occurred on the outlying Asian islands which became incorporated in the mid-Miocene into the island of New Guinea. They were able to radiate into the newly forming moist montane environments of New Guinea by virtue of having direct development on land (no free-living tadpole stage, but hatching as miniature froglets). Direct development has arisen independently in other groups of frogs in various moist mountainous regions (Goin & Goin, 1962), but is absent in other Asian microhylids. This mode of development avoids the hazards to aquatic larvae posed by fast-flowing montane streams. The Australian microhylids represent an extension of this peculiar New Guinean radiation, but in a different ecological context. In Australia their radiation is associated, not with steep mountainous regions, but with habitats where there is a shortage of suitable aquatic breeding sites. The migration from New Guinea to Australia may have been a Pleistocene event (Tyler *et al.*, 1981).

The only other amphibians in Australia are a species of Ranidae, a very recent invader from New Guinea, and *Bufo marinus*, a toad introduced by man.

Arachnids

The Australian arachnids include scorpions, spiders and mites as well as four minor groups, the Opiliones (harvestmen), Pseudoscorpionida (false scorpions), Amblypygi

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(whip scorpions) and Schizomida. The Australian harvestmen occur in three suborders, six families and about 35 genera. Most occupy temperate, humid forests with low foliage and abundant litter, although there are species from semi-arid regions or caves. Main (1981c) lists their origin as mostly Gondwanan but with some of northern, including New Guinean, affinities. Pseudoscorpions are represented in Australia by seven families, 24 genera and over 50 species. They are found primarily in temperate humid forests and sclerophyll forests where they are cryptozoic; one occurs in arid regions. Most are of Gondwanan origin although some have northern affinities (Main, 1981c). The Amblypygi and Schizomida are ancient arachnids primarily found in the humid tropics. They are represented in Australia only by a few species in the north which are probably tropical relicts (Main, 1981c). Scorpions are not diverse in Australia, comprising only three families, six genera and 29 species (Koch, 1977; 1981). The family Bothriuridae (only two Australian species) is of Gondwanan origin, the Australian genera having South American affinities. The others (Buthidae and Scorpionidae) have northern affinities and evolved from Asian stock since Australia moved northward in the Tertiary (Koch, 1981).

The Australian native spider fauna is diverse, containing 46 families and 338 genera of which 62 genera are in the family Salticidae (jumping spiders). There are three introduced families (Main, 1981c). The spiders constitute an ancient, persistent and relatively immutable group of animals. The more generalized and widespread extant families probably go back to the early Mesozoic and perhaps some of the modern genera do; some gnaphosid genera derive from the Early Jurassic.

The kinds of vertebrates that shared the terrestrial environment with some of the older genera of spiders have long since disappeared entirely or are represented today by descendants that depart so widely from their Jurassic ancestors that the relationship is evident only by virtue of the continuity of the fossil record. The significance of the great antiquity of the lower taxa of spiders is that some events influencing their modern distributional patterns may be identifiable further back in time than those affecting terrestrial vertebrates at the same taxonomic level.

Main (1981a) considers the global distribution of Australian spiders to fall into five categories, each with its own historical interpretations. They are: (1) widespread, including cosmopolitan, circumtropical and circumtemperate; (2) on southern continents; (3) Asian and/or Melanesian-Polynesian-Australian; (4) common to Australia and New Zealand; and (5) Australian only. The majority (55%) of the families are in the cosmopolitan category and most families are considered to be ultimately of northern origin (probably Pangaean). Though this classification applies primarily to families, generic examples also are given.

The Australian spider fauna has multiple origins. Taxa may be widespread for two very different reasons. Some were once continuously distributed over a large land mass which subsequently fragmented, leaving far-flung faunal relicts on the various continents, often with local ranges restricted through climatic change. Others are widespread because they disperse readily across oceanic gaps.

Many orb-weaving spiders of several families, and even some terrestrial ones, practise aerial dispersal of young spiderlings by ballooning on gossamer. In some cases, they may be carried for thousands of kilometres and intercontinental dispersal would seem to be a possible explanation of extensive distributions. Even such a cosmopolitan family as the Araneidae, however, renowned for aerial dispersal of young, has many genera with restricted distribution. Habitat and climate often may have a greater affect on distribution than dispersal

abilities. Main (1981a) concludes that only a few individual species such as *Argiope fuscata*, *Latrodectus mactans* (the Red-back) and some sparassids maintain an intercontinental distribution by aerial dispersal. Although the separation of dispersal factors from historical ones is not always possible, ballooning does not appear to adequately explain the global distribution of the widespread Australian families. Many of these widespread families (and genera) probably attained cosmopolitan distribution on Pangaea and survived in Australia throughout the subsequent fragmentation and movement of continents (Main, 1981a).

The taxa with more restricted distributions probably had a different history. About 19% of the Australian spider families have an exclusively southern distribution. Certain families and lower taxa have affinities only with other Gondwanan regions, such as South America, New Zealand, New Caledonia, New Guinea or some combination of these (Main, 1981a;b). It is tempting to speculate that these are taxa which developed in Gondwana after it split from Pangaea. Not all southern distributions, however, necessarily reflect a Gondwanan origin; some taxa, presumed to be of Gondwanan origin, were later found to be remnants of a wider Pangaean range (for example, *Hickmania* and the Symptognathidae) (Main, 1981a). Although most families of spiders appear to have an ultimate northern (Pangaean?) origin, the Migidae, Actinopodidae, Hexathelinae and families with obvious New Zealand origin are probably Gondwanan relicts. Taxa of northern origin which have entered Australia relatively recently include the family Theraphosidae and various ctenizid genera, some of which are restricted to Queensland (Main, 1981a;b;c)

Within Australia, the distribution of particular species depends on their ecological amplitude. Main (1981a) classifies the major patterns of distribution of spiders within Australia as: (1) widespread (southern continental, tropical or throughout the continent); (2) eastern Australia; (3) temperate and subtropical wet forest habitats (southeastern Australia, southwestern Australia, refugia in central Australia, isolated montane areas and riverine situations); (4) caves; (5) disjunct east-west distributions; and (6) offshore islands. Some of these patterns seem to be related primarily to present day habitat and climate. Many species are dispersed so easily that their main restriction may be presence or absence of suitable habitat.

Although particular species may have very specific requirements, as a group, spiders occupy most habitats in Australia, from the tropics to cool alpine regions, from rainforest to desert. There are cavernicolous species and others that inhabit such inhospitable places as the high tide splash zone of seashores. Their adaptive radiation is reviewed at length by Main (1981a).

Spiders have reacted to changing conditions by both kinds of responses discussed above; some remain restricted to wet refugia like rainforests and others have adaptively radiated into arid and semi-arid habitats.

Insects

Hexapods are first known from the Middle Devonian and true insects from the Late Devonian (over 350 mybp); they are an ancient terrestrial group. The Australian fossil record includes material from about 350 species of 19 orders stretching from the upper Carboniferous (about 300 mybp) to about the Pliocene (Riek, 1970a; 1974).

There are three classes of non-insectan hexapods and 26 orders, 585 families and about 54,000 species of true insects known in Australia (CSIRO, 1970) (Table 5.1). There are

many species yet to be described. Clearly, only the briefest of summaries can be given here for such a large and diverse group.

Mackerras (1970), in a review of the zoogeography of Australian insects, points out that the Archaic Element mostly consists of groups that have changed little since the Paleozoic or Mesozoic. Some are patchily distributed relicts such as the mecopteran family Meropeidae (North America, Australia), the dipteran genus *Nemopalpus* (Neotropics, Canary Islands, South Africa, Malaysia, Australia, New Zealand; fossils in Baltic amber) or the beetle genera *Cupes* and *Rhysodes* (Howden, 1981). Whether patchy distributions reflect ability to cross barriers and colonize new areas or are cases of extinction of once widespread taxa may not always be possible to ascertain. Others are not relicts, but are widespread and currently successful. Examples are the Blattodea (roaches), the lepidopteran family Hepialidae (found worldwide but with greatest development in Australia and dating back to the Cretaceous; Tindale, 1981) and many worldwide beetle genera from various families (Howden, 1981).

The Gondwanan Element has undergone extensive radiation and forms a significant faunal component of most orders of insects from Ephemeroptera to Coleoptera (Kuschel, 1960; Mackerras, 1970). This element often represents a rather early level in the evolution of those orders, for example in the more primitive sections of nearly all of the Nematocera and Orthorrhapha (Diptera). Tindale (1981) gives the lepidopterans of the superfamily Dastnioidea and Howden (1981) the scarabs of the subfamily Dynastinae and the lucanid beetles as other examples. The Old Northern Element also can be recognized among the insects as relatively old taxa that have northern affinities or affinities with India or Africa via Asia (Mackerras, 1974). Extensions of this element into Australia are mostly small, although in some cases, the extent of diversification suggests a relatively long occupancy of the continent.

The Oriental Element forms the most highly evolved and conspicuous part of almost every insect order. It has undergone considerable speciation within Australia, but comparatively little diversification at the higher taxonomic levels.

The Modern Element contains a variety of taxa characterized more by their powers of dispersal than by their geologic history. For example, some very primitive hexapods such as collembolans as well as more advanced insects like aphids and chironomid flies, because of their small size, are carried widely by air currents (Mackerras, 1970). In addition to this "aerial plankton", there are larger insects with good powers of flight that disperse widely either under their own power, such as some Odonata and Lepidoptera, or by unusual weather conditions. There is a number of cases of migration between Australia and New Zealand of butterflies (Tindale, 1981) and beetles (Howden, 1981).

Land Molluscs

The fossil record of terrestrial molluscs in Australia only goes back to the Miocene and interpretation of their early history is difficult. Bishop (1981), however, tentatively indicates the probable origins of the 24 families known from Australia. He lists six of them as widespread and probably present in Australia by the Tertiary (Pangaean?), two as very old Asian-Pacific families, seven as Gondwanan and nine as probably mid-Tertiary invaders from Asia.

The present distributional patterns are determined to a great extent by climate, vegetation and nutrients. Although there are some snail taxa that are remarkably adapted to prolonged drought, including some found in desert habitats in Australia, most land molluscs are highly sensitive to moisture loss and

Table 5.1 The taxa and geographic affinities of the known Australian hexapod fauna. Data primarily from CSIRO (1970); numbers of known species have increased since 1970 and many more remain to be described; *plus 2 superfamilies.

CLASS OR ORDER	FAMILIES FOUND ELSEWHERE BUT NOT IN AUSTRALIA	NO. OF AUSTRALIAN Families	Species
COLLEMBOLA	0	5	215
PROTURA	0	3	30
DIPLURA	1	3	32
INSECTA			
Archeognatha	1	1	3
Thysanura	2	3	23
Ephemeroptera	7	4	124
Odonata	8	16	248
Blattodea	1	4	439
Isoptera	1	5	182
Mantodea	6	2	118
Dermoptera	2	5	60
Plecoptera	3	4	84
Orthoptera	13	13	1 513
Phasmatodea	0	2	132
Embioptera	5	3	65
Psocoptera	6*	21	120
Phthiraptera	5	10	208
Hemiptera	16	88	3 661
Thysanoptera	2	3	287
Megaloptera	0	2	16
Neuroptera	2	15	396
Coleoptera	38	114	19 219
Strepsiptera	0	5	93
Mecoptera	2	5	20
Siphonaptera	8	9	68
Diptera	28	87	6 256
Trichoptera	6	18	260
Lepidoptera	29	76	11 221
Hymenoptera	14	59	8 834
TOTAL	206*	585	53 927

are found in relatively wet, shady environments. Much of the Australian environment is inhospitable and numbers of species in any given area are not high by world standards (Bishop, 1981). The deficiency of Australian soils in nutrients such as nitrogen, phosphorous and calcium (see Chapter 4, this Volume) affects snails and may limit their distribution. Shell formation, for example, requires considerable calcium. The eastern coast of Australia has the most eutrophic soils and provides forest habitat with adequate moisture and shelter. This area, not surprisingly, is the most favourable in Australia for terrestrial molluscan life (Bishop, 1981).

Oligochaetes

Oligochaetes are in three orders, the Lumbriculida and Tubificida (microdriles) and the Haplotauxida (earthworms). Collectively, they are represented in Australia by 10 of the 25 worldwide families. The native terrestrial oligochaetes, however, involve only two families, the Enchytraeidae (Tubificida) and the Megascolecidae (Haplotauxida). The remainder are either widespread anthropochorous species or are aquatic and hence outside the scope of this Chapter.

The enchytraeids are known so poorly in Australia that little can be deduced of their history, affinities or distributions.

Both Australian subfamilies of megascolecids, the Acanthodrilinae and Megascoleciniae, have nearly worldwide distributions (though largely excluding the Palaearctic) which

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may reflect a former Pangaean distribution. The lower taxa of both subfamilies, however, in Australia have strong affinities with other southern areas and particularly so with New Zealand and New Caledonia. Affinity with India is especially interesting. The non-pheretimoid part of the tribe Megascolecini occurs both in India and Australia. Since India was the first major land mass to separate from Gondwana, the taxon must be ancient. Yet, this group is absent from Africa and South America which separated from Gondwana later. These earthworms may have had a restricted distribution on Gondwana that included the Australian-Indian segment, but not the African-South American one (Jamieson, 1981).

Other than general Pangaean relationships, the affinities with northern regions are slight. A post-Miocene inflow of pheretimoids (tribe Megascolecini) from Asia is still in progress. Movement has been greater in the opposite direction, as two tribes, the Dichogastrini and Megascolecini, have representatives that invaded the Oriental Region from Australia (and India) in the Cainozoic and spread as far as China and Japan (Jamieson, 1981).

In summary, some Pangaean earthworm elements reached Australia via Gondwana where they diverged in isolation; later there was a small two-way exchange with Asia in the Cainozoic.

Other Taxa

There are some terrestrial groups that have not been discussed, either in the above Section treating individual taxa or in the general discussions of the various faunal elements. Some of these have been mentioned briefly by Main (1981c) who notes that some of the centipedes are of Gondwanan origin, some of Old Northern and some of more recent northern derivation.

Others, including terrestrial flatworms, leeches, mites, tardigrades, protozoans and many insect groups have not been reviewed in the context of modern ideas of plate tectonics. Their taxonomy and distribution is inadequately known.

THE AUSTRALIAN TERRESTRIAL FAUNA IN A GLOBAL PERSPECTIVE

The virtual isolation of Australia from other continents during its northward movement between the Late Paleocene and the Miocene and its partial isolation from the Miocene to the present time has resulted in a terrestrial fauna that is unique in several ways.

The taxonomic composition of the Australian fauna differs from that of other continents. In many cases, a taxon of a comparatively low level has radiated adaptively in Australia in much the same way as another taxon of the same Class has radiated elsewhere. For example, marsupial mammals take the place of eutherians, elapids the place of colubrids and so on. Such replacement may even occur at higher taxonomic levels. The significance of these taxonomic "imbalances" is discussed below.

Missing Or Poorly Represented Taxa

There are two scenarios that may be invoked to account for a missing or depauperate taxon in Australia. One is that the taxon originated elsewhere after the fragmentation of Australia from Gondwana and either has not reached Australia subsequently (missing taxon) or has only done so recently and has not had sufficient time to spread, adaptively radiate and diversify (depauperate taxon). The second is that the

group was present at the time of separation, but subsequently became extinct in Australia and has not (missing taxa) or has only recently (depauperate taxa) reinvaded the continent.

Whether missing taxa have been unable to reach Australia or whether they have arrived (or do arrive periodically) but fail to establish may not always be clear. In the latter case, the physical environment may be different from that of the place of origin and to which they are adapted or they may find a favourable physical environment, but be unable to compete successfully with already established species. Clearly, detailed ecological studies would be required to resolve such hypotheses.

Taxa that clearly belong to Scenario 1 would be those whose fossil record indicates they did not originate until after Australia separated from Antarctica and whose pattern of distribution in Australia would suggest recent entry. There are a number of examples that fit this combination of characteristics, including most of the modern and some of the Asian Tertiary Elements.

The frog genus *Rana* (family Ranidae), for example, is known first from the Miocene of Europe and Asia and the Miocene, Pliocene and Pleistocene of North America (Dowling & Duellman, 1974-78). Extant members of the genus are nearly cosmopolitan although they are represented poorly in South America and do not occur at all in the southern part of that continent. The sole Australian species, *Rana daemeli* (closely aligned with the New Guinean *R. papua*), occurs only on Cape York Peninsula (Cogger, 1979). This genus (and probably the subfamily Raninae) thus originated after Australia had separated from the rest of Gondwana. Only one species succeeded in reaching Australia and then only recently, having scarcely diverged from the New Guinean form.

The turtle family Carettochelydidae now consists of only one species, *Carettochelys insculpta*, found in the rivers of the southern coast of New Guinea and in a few rivers in the Northern Territory. The fossil record of this family goes back to the upper Cretaceous to Oligocene of Europe and North America and to the Miocene in New Guinea. This suggests that the family originated in the north but did not reach Gondwana, but rather, arrived in New Guinea from the north by the Miocene and only recently reached Australia from New Guinea (Scenario 1). It is probable that previous post-Tertiary invasions may have occurred as there are fossils that may be *Carettochelys* from the Pleistocene of Windjana Gorge, Western Australia (Molnar, 1983a).

Some old groups seem to belong to Scenario 1. Several widespread groups of earthworms are absent in Australia. All of the families of the Lumbricoidea (except for introduced species) are absent, even though the group probably originated in the Triassic or earlier. Similarly, the family Ocnerodrilidae, supposedly Pangaean and with probable origin in South America-Africa is not in Australia. Jamieson (1981) suggests that Australia may not have been warm enough in the Mesozoic to support this heat-loving group. The lack of a fossil record ensures that much of this remains speculation; why these worms are not part of the Australian fauna is a mystery.

Eutherians are very depauperate in Australia. Of the world's terrestrial orders, 11 are missing from Australia, though most are distributed widely elsewhere. They probably never reached Australia, not surprising in light of the fact that only one stock of marsupials (the microbiotheriids) did. Gondwana, perhaps because of its archipelagic nature, does not seem to have been a continent easily crossed by mammals. The three orders of eutherians that did reach Australia came in the Tertiary or later, have not radiated extensively and are depauperate by world standards.

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Amphibians are represented poorly in Australia at the higher taxonomic levels. Of the four extant orders, three, Gymnophiona (caecilians), Caudata (salamanders) and Meantes (sirens) are absent and probably were never there. Even the Anura, the only order present, is represented by only two families with extensive radiations and two depauperate ones which are relatively recent arrivals.

The softshell turtles (family Trionychidae) do not occur now in Australia although they are widespread in Asia, Africa and North America (Bellairs, 1969; Dowling & Duellman, 1974-78) and are known as fossils from South America. Their fossil record dates back to the Jurassic (Molnar, 1983a). Hence, they antedate the breakup of Gondwana and were distributed in southern continents. Trionychids are known from the Pliocene of Queensland (Molnar, 1983a; Molnar, 1984b), that is, well after Australia had separated from Antarctica. Softshell turtles probably were part of the Gondwanan fauna that persisted in Australia after it became isolated, but became extinct and have not succeeded in re-establishing in Australia in modern times. They provide a clear example of Scenario 2. Because of the poor fossil record, other taxa whose absence may be accountable by Scenario 2 are difficult to identify. Indeed, if the few fossils of trionychid turtles had not been found in Australia, that family would probably be allocated to Scenario 1 rather than Scenario 2.

Examples of missing fauna which cannot be assigned confidently to either Scenario are: two orders of insects, Zoraptera (Smithers, 1970) and Grylloblatoidea (Key, 1970), the stonely suborder Setipalpi (Riek, 1970b), flies of the ancient and widespread family Ptychopteridae (Colless & McAlpine, 1970), several otherwise worldwide groups of Hymenoptera (Riek, 1970c), a number of spiders, the arachnid orders Solpugida (sun spiders), Uropygi (whipscorpions) and Ricinulei (Main, 1981c) and the reptilian order Rynchocephalia (Tuatara).

Adaptive radiation is apt to produce endemic lower taxa within any continent. The absence of taxa at the familial or lower level is not remarkable unless they occur on most other continents except Australia.

Endemism

On any continent, or even smaller geographic unit, one would expect a high degree of endemism at the specific and generic levels and that such is also the case for Australia is of little intrinsic interest. The taxa that are endemic at the familial level or above are of most interest and emphasized here.

In considering the topic of endemism, sometimes Australia and New Guinea may be usefully linked because these two regions have been connected by land repeatedly in the Pleistocene, most recently only a few thousand years ago. There has been insufficient time since the most recent separation for extensive divergence of populations isolated on opposite sides of the Torres Strait.

There are two processes whereby endemism can occur. One is the failure of an autochthonous taxon to reach other areas. The second is extinction of a taxon in parts of its geographic range, leaving it extant only in one area as a geographical relict (Darlington, 1963). The area in which it is endemic is not necessarily the one in which it had its origin (it may be either autochthonous or allochthonous). These two kinds of endemism are designated Originative Endemism and Extinctive Endemism, respectively.

Extinctive Endemism: Extinctive endemism probably is much less common on a continental basis than originative endemism, particularly for a relatively isolated continent. If monotremes originated outside Australia, which is doubtful, they would be examples of extinctive endemism.

Originative Endemism: The long period of relative isolation of Australia during its northerly movement provided an opportunity for the old Gondwanan fauna trapped on it to diverge from their relatives on other fragments. In some cases, that divergence was relatively slow and only reached the generic level. The turtle family Chelidae occurs both in Australia and South America, but the two continents have different genera (Dowling & Duellman, 1974-78).

The marsupials are perhaps the best vertebrate examples of endemism at the familial level. All 14 of the Australian marsupial families are indigenous in Australia or to Australo-New Guinea and none has ever been found as fossils on any other continent. They are true endemics, having originated in the Australian Region and (except for a few introductions of them by man elsewhere) have never been established on other continents.

The avian families Menuridae (lyrebirds) and Atrichornithidae (scrub-birds) clearly originated in Australia and have never dispersed elsewhere.

The reptilian family Pygopodidae is found only in Australo-New Guinea. It is believed to have evolved from geckos in southwestern Australia, where the greatest number of genera occur and species density is greatest (Fig. 5.10; Cogger & Heatwole, 1981).

Whether Australo-New Guinea has any endemic families of amphibians depends on which side of current taxonomic debate one elects to support. Clearly, the two major radiations of frogs took place *in situ* and represent either endemic families or subfamilies, according to one's taxonomic taste.

Table 5.2 indicates the endemism of various taxa of Australian animals at different levels. The taxonomy is not sufficiently known for many groups. Other than the expected increase in proportional endemism from higher to lower taxa, the main point to be made is that endemism at the generic and specific levels is high and that non-eutherian mammals have high endemism, even at the familial level.

Community Structure

Australian communities differ in structure from one locality to another. They may be analysed in terms of the environmental factors influencing such structuring and compared with equivalent communities elsewhere.

Geographic Variation. Communities change geographically. The number of organisms tends to decrease from low latitudes toward higher ones and from moist habitats toward drier ones. For example, the total number of species in a tropical rainforest is far higher than in the same hectarage of alpine heath or stark desert. This pattern holds true in a general way for some individual taxa as well, but regional peculiarities in climate, soil, vegetation or other conditions may impose modifications.

For certain taxa, geographic trends in species richness may be just the opposite, with the greatest number of species being found in deserts or at high latitudes or altitudes. In Australia, some groups, like reptiles, have the greatest numbers of species in the tropics, but species richness of birds and mammals of various taxa either have the reverse trend, exhibit no relation to latitude or have lowest values at intermediate latitudes. Individual taxa within a Class differ in

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Table 5.2 Endemism of the Australian terrestrial fauna. Groups selected on the basis of the completeness with which they have been studied and on the availability of summaries in the literature. (Data from CSIRO, 1970; Cogger, 1975; Keast, 1981; Strahan, 1983; Archer & Clayton, 1984; Jarman, pers. comm; van Dyke, pers. comm.)

TAXON	PERCENTAGE OF AUSTRALIAN ANIMALS THAT ARE ENDEMIC AT THE LEVEL OF:			REMARKS
	Family	Genus	Species	
MAMMALS				
Monotremes	50	50	50	all non-endemic taxa shared only with New Guinea
Marsupials	53	46	89	all non-endemic species shared only with New Guinea
Placentals	0	33	73	mainly bats that aren't endemic
BIRDS	11	37	71	many more taxa are endemic to Australia and New Guinea combined
REPTILES	0	55	88	not including sea-snakes and sea-turtles; two families endemic to Australia and New Guinea combined
AMPHIBIANS	0	79	94	
INSECTS				
ORTHOPTERA				
Acridoidea	—	90	—	
Grylloidea	—	25	—	
Other superfamilies	—	50–60	—	
PHASMATODEA				
Phasmatidae	—	> 50	nearly all	
LEPIDOPTERA				
Papilionidae	—	17	24	
Pieridae	—	0	64	
Coliadinae	—	0	25	
Pierinae	—	—	—	
Nymphalidae	—	—	6	
Danainae	—	—	83	
Satyrinae	—	50	—	
Nymphalinae	—	—	4	
Lycaenidae	—	28	61	
Theclinae	—	14	37	
Polyommatinae	—	0	0	
All other families and subfamilies	—	—	—	
COLEOPTERA	0	75	—	
ARACHNIDS				
Spiders	2	26	—	
Scorpions	0	75	79	
LAND SNAILS	4	—	—	
EARTHWORMS				
Megascolecini	—	71	—	

pattern. In some cases, there is an overriding relation to moisture: numbers of species of birds and frogs have a positive correlation with rainfall, for example. When tropical and temperate areas of equivalent rainfall are compared, there is still a greater richness of some reptiles in the tropics, but the reverse is true for mammals and frogs; some groups of lizards show no difference. Certain lizard groups increase in species richness with increasing mean annual hours of sunshine (Pianka & Schall, 1984). Hall (1984) shows that numbers of species of bats decrease in Australia with increasing latitude and at a given latitude is lower in the drier regions than in humid ones.

Vegetation complexity may be involved for some taxa. Species richness of birds is greater in habitats with a larger number of horizontal layers of vegetation (Keast, 1981b).

Other biotic factors may be significant in either a positive or a negative way. There is a tendency for certain species to associate, even over a range of environmental conditions (Kikkawa *et al.*, 1981) and they may be responding to each other as well as other environmental factors. Conversely, some taxa have inverse relationships. In various deserts, including those of Australia, numbers of birds and numbers of lizards are inversely related and may reflect competition between members of these two groups (Pianka & Schall, 1984).

Because different taxa have different patterns of species density, clearly not only are there going to be geographic changes in numbers of species, but also in the relative proportions with which various taxa are represented in regional communities. That is, taxonomic composition of communities varies from place to place. One of the most important and controversial issues in modern ecology is the extent to which difference in species composition affect the way communities function.

Ecological Equivalence. Given that in different geographic regions similar climates exert the same kinds of selective pressures, adaptive radiation may follow similar trends, with convergent evolution resulting in genetically different species with similar morphological, ecological and physiological adaptations. Unrelated taxa which share common adaptive attributes through parallel evolution are called ecological equivalents. Sometimes the parallels are striking, both at the level of the individual taxon and the whole biotic community. A number of examples of ecological equivalence between taxa from Australia and other continents has been outlined (see Heatwole, 1970; Pianka & Pianka, 1970, for reptilian examples). At the level of the entire biotic community, tropical rainforests, for example, have a similar appearance and structure (several canopy layers, vines, lianas, vascular epiphytes) in all continents, although the structural units are made up of different families or genera in the different areas. Whenever certain conditions of temperature and moisture prevail, unless limited by soil conditions, tropical rainforest develops in time. The various structural elements evolve from whatever taxonomic units are at hand.

Comparisons of communities of the same biome (*e.g.* tropical rainforest, desert) from different continents permit assessment of the role of evolution in community structure. The few faunal comparisons that have been carried out have produced the surprising conclusion that most continents are similar to each other, with the exception of Australia which is unique in some respects. Lizard assemblages have been subjected to intercontinental comparisons (reviewed by Heatwole, 1976; Heatwole, 1982; Pianka, 1981). Australian deserts have a greater number of species of lizards per locality than does either the Kalahari or American deserts, the latter two being nearly the same. Part of the explanation is that habitats such as sandridges, mulga and sand plains interdigitate more in Australia and a given locality may encompass several habi-

tats. Also, within a habitat, Australian species show more specialization for particular microhabitats and a greater number of species can be accommodated (for example, 10 species in Australian sandridges compared to only one in the Kalahari). The more constant climate of Australian deserts may permit the species to divide up the day into a greater number of suitable activity periods and accommodate more species in that way. Finally, lizards seem to have usurped the ecological roles played by some worms, insects, snakes, birds or mammals in other deserts. There are fewer species of ground-nesting insectivorous birds in Australian deserts than in the Kalahari and their numbers seem to have been replaced by species of lizards. When different localities within Australia are compared, there is an inverse relationship between numbers of species of lizards and ground-nesting insectivorous birds. There must be a balance between these two ecologically similar groups; if there are more species of one, there must be fewer of the other.

In contrast to deserts, the rainforest fauna has fewer reptilian species in Australia than in other continents (Heatwole, 1981). Perhaps wet-adapted species suffered greater extinction rates in the past when moist refugia were restricted or eliminated by expanding aridity.

Morton (1979) compared Australian and North American deserts and found that the latter had more species of mammals (109) than the former (73) despite the area of desert being greater in Australia. The difference lay mainly in the greater abundance of granivorous mammals (mostly rodents) in North American deserts. In Australia, there is a preponderance of seed-gathering ants and granivorous birds.

By contrast, there are more species of insectivorous mammals, birds and lizards in Australian deserts than in North American deserts, perhaps because of the abundance of ants for food.

With a paucity of small mammal species to serve as prey, there are relatively few mammalian carnivores in Australian deserts. The role of predation upon the rich lizard fauna is performed by carnivorous lizards, especially varanids, rather than by mammals.

Ants play a particularly important role in Australia, where they are responsible for the dispersal of about 1,500 species of vascular plants, as opposed to ≈ 300 species in all the rest of the world (Berg, 1975). Ants often control the composition of much of the rest of the insect fauna. A quantitative assessment of the structuring of Australian ant assemblages and comparison with that of other continents would be extremely valuable.

There also are differences in the trophic structure of avian assemblages on different continents. In this respect, Australia is like most continents in having bird species specialized as nectar feeders and pollinators. Europe differs and is depauperate in flower-visiting birds compared to similar climatic regions in Australia. Ford (1985) advances the hypothesis that in Europe, nectarivorous birds were pre-empted by social bees. There is a greater propensity for frugivory among birds from wet habitats and a stronger tendency toward granivory among those from dry ones.

Eventually some species fills each of the niches characteristic of a given biome, even if the taxa which are modified vary from one locality to another. Ecological equivalents, thus formed, are often from the same high level taxon, say Class or Order, but with parallel evolution occurring between different families (*e.g.* ecological equivalence in the Class Reptilia between the family Agamidae in Australia and the family Iguanidae in America). If taxa from the group are not available, however, quite different genetic entities may become ecological equivalents (*e.g.* seed-collecting ants and

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grain-eating rodents; insectivorous birds and lizards). Ecological equivalence seemingly develops more easily among related taxa, but does occur in genetically very different ones.

HUMAN INFLUENCE

Extermination by direct methods is often difficult to achieve. Population densities of target organisms are reduced, but complete extinction is nearly impossible for many species. Unsuccessful attempts to exterminate many "pest" species in Australia through shooting, trapping, poisoning and other methods have resulted in temporary control but not complete extermination. The largest kangaroos continue to thrive despite heavy shooting pressure in many areas. These eurytopic species are among the most difficult to eradicate and are problems partly because they are ecologically flexible and succeed in invading human habitats. Other species are much more sensitive.

Australian vertebrates probably exterminated by direct means by Europeans are *Thylacinus cynocephalus*, which was hunted for bounty (but see Chapter 20, this Volume), the Toolache Wallaby (*Macropus greyi*), also hunted for bounty (Calaby, 1984), and three insular forms of small emus (Archer, 1984f). Improved legislation and increased public awareness may prevent any further instances of this kind (see Chapter 11, this Volume).

There has been speculation that early Aborigines may have been responsible for the extinction of many of the larger Australian native mammals at the close of the Pleistocene (but see Chapter 10, this Volume).

In contrast to direct methods, introduction of exotic fauna and habitat destruction have been very important in eliminating species from the Australian fauna and in endangering the survival of others. The traditional use of fire by Aborigines for many millennia altered vegetation and may have contributed to the extinction of some animals (Archer & Aplin, 1984).

A great proportion of the Australian continent has been affected by human activity (Adamson & Fox, 1982). European-style agriculture and pastoralism have, in a few cases, led to improved conditions, at least temporarily, for a variety of native mammals that flourished and became sufficient pests in crops and pastures to attract bounties. They included various kangaroos, wallabies, rat-kangaroos and (briefly) wombats and bandicoots. In most cases, they became extremely abundant following human modification of the landscape, then, like the introduced species, suffered a decline to a lower level around which populations have since fluctuated (Jarman & Johnson, 1977). The Ord River scheme provided greater food resources for corellas and magpie geese which became a nuisance (Beeton, 1977). Birds that inhabit open areas (e.g. Willie Wagtail) probably benefited from human activities. Construction of artificial bodies of water by humans has created breeding sites for some frogs (Tyler, 1979b). Usually, however, pastoralism and agriculture have led to a degradation of habitat. Clearing of habitat leads to local extinction of all but the most eurytopic species and when drastic modification occurs over extensive areas, as it has in Australia, entire species are lost. For some species, offshore islands still unmodified by agriculture, are the only remaining refuges.

Calaby (1984) estimates that 15 vertebrate species (one bird, seven marsupials and seven native rodents) have become extinct in Australia since European settlement; many more are on the endangered list. Archer & Aplin (1984) note that 16 species of marsupials have become extinct, at least locally, in the State of New South Wales. The greatest extinction occurred on the open plains, where 43% of the species were

lost. Less devastation occurred in woodland savannah (13%) and sclerophyll forest (8%) and no species are lost from rainforest. These different intensities of extinction may be related to the relative degree to which these habitats have been modified by man, his domestic animals and inadvertently introduced exotics. Those species that have survived extreme habitat alteration are probably able to cope with the modified conditions and now are relatively safe. Paradoxically, the rainforest species are now at greater risk than those of the more open habitats; they cannot survive habitat alteration and many of their rainforest refuges are at risk.

Habitat destruction may occur in ways that are not as obvious as direct clearing. Forests and woodlands in many parts of Australia are declining alarmingly and the phenomenon is referred to as "dieback". There is debate as to whether this is a "natural" phenomenon or induced by human activities; the causes are probably different in different regions. Such diverse factors as intensity and nature of land use, root pathogens, insect defoliation and attack on roots, drought, salinity, senescence and nutrients, variously or in combination, can be associated with the malady (see review by Heatwole & Lowman, 1986). Whatever the cause, the significant habitat alteration affects birds (Ford & Bell, 1981) and reptiles (Crome, pers. comm.) at least.

A more insidious threat to the Australian fauna than habitat destruction is pollution. In contrast to clearance or drastic modification of habitat, the effects of pollution are not as readily visible, but are potentially as destructive. The same scientific procedures that produced the technology necessary to support burgeoning human populations in the first place, must be applied to the solving of this and related problems. If that is successful, perhaps the animal diversity of Australia can be maintained.

OVERVIEW

The different elements of the fauna may show different distributional patterns. The old Gondwanan fauna has been in Australia a long time and has had a longer time to disperse and, at least at some taxonomic levels (genus, family), would be expected to have broader distributions. As past climates changed, some Gondwanan taxa were able to adapt gradually to those changes. A combination of radiation into new habitats and adaptation to changing conditions led to diversification. The marsupials constitute a prime Australian example. Other taxa of Gondwanan origin lacked flexibility in adapting to changing conditions and became relicts, whose ranges became progressively more restricted as their habitats shrank. Relict taxa became widely separated in ever-dwindling refugia.

Between these two extremes lies a continuum of intermediate conditions. One feature that all of them show, in contrast to many of the newer elements, is that their distributions do not reflect their point of entry into Australia. They have been there so long that their Gondwanan distributions have been blurred by later geological and climatic events and adaptive radiations.

The Asian Tertiary Element may share some of these characteristics. Adaptive radiation does not proceed uniformly in time or among taxa. Rather, particular taxa in certain periods seem to expand into new habitats and lifestyles with remarkable rapidity. In other cases, only slight change occurs over many millions of years. The interactions of changing ecological conditions and genetic factors probably account for these differences. Whatever the reason, rapid adaptive radiation by an Asian Tertiary Element could lead to diversification within a taxon and a collective widespread distribution of its derivatives. Tertiary incursion into Australia could have produced distributional patterns similar to those mentioned

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for successful Gondwanan elements. Secondary centres of speciation and adaptive radiation could mask the effect of the entry point, especially in the older of the Tertiary elements. They, too, have been in Australia long enough to radiate into new habitats and have experienced a kaleidoscope of changing conditions that alternately caused isolation and permitted migration. The newer Tertiary elements and especially the Quaternary ones, however, have not had time to spread far from their point of entry into Australia. They have experienced fewer oscillations of climate. Consequently, there have been fewer occasions of unusually favourable conditions that might have permitted them to cross areas currently acting as dispersal barriers; nor have they had sufficient time to adapt to the conditions of such barriers and radiate into new habitats. As one proceeds from the older to the newer elements, distributional patterns increasingly reflect the points of entry into Australia and the present day climate and vegetation, but decreasingly reflect past climatic changes and the opening and closing of barriers within the continent.

In a very general way, the older elements have a greater diversity than equivalent taxa among the newer elements. There are, of course, variations imposed by different rates of adaptive radiation among taxa and relict or declining taxa do not conform to the trend.

Climate, habitat and history are not the only determinants of distributional patterns. Various interactions with other species may have an effect. A species may be eliminated by predation, parasites or competition.

Humans have had a great effect on distributional patterns, directly through introduction of species and indirectly through the effect these species have had on native fauna. Humans also limited distributions or caused extinction through overexploitation, habitat destruction and pollution.

Important in a study of the fauna of a continent such as Australia is to list what kinds of animals are present, where they come from, when they came and where they now occur. Also important is the assessment of the relative roles of climate and vegetation (past and present), geological history, palaeogeography, biotic interactions and human interference as determinants of observed distributions. This Chapter has broadly outlined some of the historical and ecological factors influencing the distribution of the terrestrial fauna of Australia. Further volumes in this series will treat these topics in depth and in reference to individual taxa.

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6. EVOLUTION AND RADIATION OF THE TERRESTRIAL FAUNA

A. R. MAIN

INTRODUCTION

The history of the continent outlined in Chapter 1 indicates that many different events, ranging in time from the distant past to the present, have influenced Australia and its fauna. In its composition the Australian terrestrial fauna is more like that of an island than a typical continent. Is this due to: i) the lack of variety present in the original fauna, ii) the long isolation of Australia, iii) the few faunal elements which entered Australia after its contact with Asia in the mid-Tertiary or iv) extinctions resulting from climatic and environmental change? If there were extinctions, what effect have they had on the remaining fauna? Has there been ecological release of what did survive?

Answers to the foregoing questions are relevant for any interpretation or understanding of the evolution and radiation of the terrestrial fauna. There has been scope for a multitude of responses and interactions, but the nature and extent of these are not clear. The questions posed are addressed under the following relatively artificial headings: origin or derivation; adaptations; divergence; radiation; extinctions. These are not mutually exclusive categories and clearly divergence and radiation may represent aspects of the same phenomenon.

Two recent publications, Keast (1981) and Archer & Clayton (1984), have treated or alluded to many of the above topics. This Chapter looks at the same phenomena from a different perspective.

Background and Generalities

Evolution of the Australian fauna is basically a population phenomenon which can be viewed on several spatial and temporal scales: local, regional, continental; or present, recent or distant past.

The problem is how to incorporate population genetics theory into an explanation of the present fauna. The characteristics of the populations present when plate movements and climatic changes occurred are essentially unknowable.

Ideally, any hypotheses erected should be testable, but should be no more complicated than needed to account for or explain the facts or observations. This has great significance in evolutionary studies because there is no logical necessity for an evolutionary or adaptive response to every challenge to be identical or simple. There is always an element of chance, be it in respect of the variability of the gene pool, gene flow, the size of the population or the intensity and duration of selection. Simple explanations may not be adequate. Multiple causes may operate, as clearly has happened with the evolution of the Australian fauna.

The world of an organism is one in which aspects of the physical environment interact with biological factors, such as competitors, predators and disease, which make life more or less difficult and so alter the chance of survival and successful reproduction. Hutchinson (1957) seeks to advance understanding by considering all factors which affect an organism

as constituting a space with N axes. The extremes of these axes define an N dimensional space within which an organism, in the absence of competitors, predators and disease, could survive and reproduce. This space Hutchinson terms the fundamental niche of the organism. When an organism has to contend with competitors, predators and disease, the space which can be occupied successfully is reduced. This lesser space Hutchinson terms the realized niche.

Field distributional patterns reflect the expression of the realized niche. The fundamental niche may be such that, under other biological circumstances, patterns of distribution may be quite different. Such differences are particularly apparent with introduced pest species which invade a much wider range of habitats than would be inferred from their original range. The present Australian continent represents a palimpsest; the extant fauna reflects responses to past and current ecological and environmental stresses. In many cases, clear-cut choices between alternative evolutionary and ecological hypotheses are not possible (Quinn & Dunham, 1983). It would be remarkable if our present knowledge was sufficient to untangle all these effects or produce definitive hypotheses.

Summary Model

At least, a list can be made of the factors and constraints which should be taken into account when interpreting the evolution of the Australian fauna.

1. Australia was formerly part of Gondwana. It broke from Antarctica in the early Tertiary.
2. Ancestral populations of some of the present fauna may have been present on the continental plate at this time.
3. Australia was isolated from the time it separated from Antarctica until collision with Asia in the Miocene.
4. During this isolation, the populations of the original faunal elements evolved in response to changing environmental conditions.
5. After Miocene times, faunal elements of Asian origin could have become established in Australia.
6. Subsequent to the establishment of the circumpolar current in the mid-Oligocene, Australian climates commenced an arid deterioration which has continued to the present.
7. The evolutionary responses of both the Gondwanan and the newer post-collision fauna has been effected by (a) nature and intensity of selection; (b) ecological opportunities; (c) gene flow within and between populations; (d) population size; (e) genetic diversity within the population; (f) breeding biology.
8. The effect of each of these factors may have varied over time and between populations.

ORIGIN OF FAUNA

Criteria for Determining Possible Origins

Historical: Within the present fauna, several elements can be recognized by their relationships to the faunas of other continents: (a) those whose affinities are with similar groups in other southern continents; (b) an autochthonous group with no discernible relationships elsewhere; (c) those with relationships to Asia; and (d) a very diverse group of exotics derived by accidental or deliberate introductions by man since European settlement. Elements except (d) of the above can be considered indigenous fauna.

The Australian fauna has always been considered depauperate or unbalanced. This characteristic can be understood only in terms of time and place of origin and possible means of dispersal to Australia. Establishment of the time and place of origin also permits comparative studies of the evolution of the ancestral and colonizing stock and calculation of rates of evolutionary change. Such studies theoretically are possible for both recent introductions and those of the distant past.

Whilst recently introduced fauna should be easiest to study with respect to the above, in practice there has been little work except in those cases where introductions have reached pest status in Australia. In the latter, biological studies in the place of origin have become desirable so that control measures of the pest population can be implemented.

The indigenous fauna is much more difficult to investigate in the above context. That component with southern affinities is most difficult of all. Nevertheless, this component recently has received the most attention. In part, this has been due to the intrinsic interest of these old groups. More importantly, the wide acceptance of continental drift means that the times of isolation can be established or inferred by dating the lavas exposed as a consequence of plate fracture and subsequent sea floor spreading. Notwithstanding, the nature of the alternative current or earlier interpretations needs to be kept in mind lest they be rejected too readily as completely untenable or not parsimonious. A summary of past interpretation in the light of the current standards follows.

Older interpretations of the origin and composition of the indigenous fauna have been based on one or some of the following assumptions:

(a) The present land masses always have existed in their present situation. That evolution of morphologically advanced and ecologically aggressive forms would take place on large land masses with diverse topography and fauna.

i. As new faunal elements evolved in the large landmasses, "older elements" would be pushed to the periphery which effectively meant into the "peninsulas" of Africa, Australia and South America (Matthews, 1939; Darlington, 1965; 1971; Mayr, 1972). This would account for the distribution of marsupials and ratite birds.

ii. Visualizing transient land bridges which permitted some faunal elements from the larger land masses to cross what were formerly or are at present wide oceans or seas, for example, Bering Bridge (Simpson, 1947), Isthmus of Panama or other connections made possible by fluctuations of sea level during the Pleistocene.

iii. Dispersal across barriers, for example, tectonically active areas or island arcs which act as island stepping stones for island hopping fauna (Simpson, 1961).

(b) The present land masses are not fixed, but move about or drift (Wegener, 1967; du Toit, 1973). From this assumption is derived the hypothesis that common southern distributions

represent elements once widespread on a former continent which subsequently fragmented, each fragment carrying part of the former widespread fauna.

The theories under (a) have in common that they sought simplicity or parsimony in making explanations in terms of the currently observed distributions of land, with only minor changes such as are known to occur in tectonically active areas as with the shoaling of banks to form islands, or changes in sea level. Testability in such cases was limited to congruence of dispersal events and changes in islands or sea level.

The explanations based on continental drift still sought simple explanations, but in effect stated that all the faunal observations could not be explained readily unless continents had drifted by some unknown mechanism. This last supplementary hypothesis prevented the acceptance of continental drift as an explanation of the observed southern distribution of some faunal elements. Matthews (1939), Simpson (1943) and Darlington (1965) were particularly sceptical of continental drift as an explanation of observed distributions. Non-acceptance continued until plate tectonics emerged as an explanation of the present distribution of continental and ocean crust, deep sea trenches and the world pattern of seismicity.

Constraints: The demonstration that plates have moved, along with the ability to date the formation of new ocean floor, has led to a belief among some biogeographers that this date gives a precise time for the division of the former continental fauna into separately evolving faunas. The date of plate movement, as evidenced by sea floor spreading, is taken as the date of divergence of southern faunas. It is, indeed, the last date at which overland dispersal would be possible if the fracture occurred on dry land, but the first land fracture may precede sea-floor spreading by many millions of years (Craddock, 1982). To see whether this is likely to be the case is pertinent for Australia.

The present boundaries of the Australian Plate and past connections to other parts of Gondwana are as follows: to the south of Australia, it is East Antarctica. This is a continental fracture, dated as Late Paleocene (Crook, 1981). To the island arcs to the north, it is an active collision junction with the Australian Plate descending (Powell *et al.*, 1981). The junction between East Antarctica and West Antarctica is unknown in detail, but is believed to be a continental connection. The present surface of West Antarctica, when isostatically adjusted for the overlying ice cover, shows that it is fragmented into an archipelago by deep marine channels or basins. This breakup of West Antarctica is thought to be late Cainozoic but possibly began in the Oligocene (Katz, 1982). The volcanoes associated with the breakup rest on a pre-volcanic erosional surface which is exceedingly flat in most places and appears to have developed in the Late Cretaceous or early Tertiary (Le Masurier & Rex, 1982).

Connections: Australia, Antarctica, South America: The connection between West Antarctica through the Antarctic Peninsula to South America is complex. At least three plates are involved: those associated with the Pacific, Antarctic and South America.

The separation of Antarctica and South America is possibly the last major event in the breakup of Gondwana. Dating this event, however, is difficult. Some authors have seen the similarities in the fold belts of the Andes and the Antarctic Peninsula (Antarctandes) (Dalziel, 1976). Hamilton (1967) recognizes West Antarctica as an archipelago, but visualizes earlier connections with South America as a narrow continental bridge. Dalziel & Elliot (1971) postulate a narrow connection in the early Tertiary. But Miller (1982) and Katz (1972) do not follow this interpretation and Dalziel (1982)

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wonders whether the similarities are due to contemporary processes rather than disruption of a continuous mountain chain.

Barker & Burrell (1977; 1982) date coherent sea floor spreading in Drake Passage as beginning about 29 mybp and the Antarctic Circumpolar Current as fully developed about 23.5±2.5 mybp, that is, at about the Oligocene/Miocene boundary.

Covacevich & Rich (1982) report tracks of a terrestrial bird, possibly a ratite or phororhacoid, in lacustrine deposits dated on plant remains as of Oligocene or Miocene age on King George Island on the southern side of Drake Passage. This demonstrates that terrestrial vertebrates were present at a place along the possible Antarctic dispersal route in the Tertiary. More accurate dating is needed, in the light of the findings of Barker & Burrell (1982) above, in order to clarify whether at the time the tracks were made the birds: i) could still make contact with South America, ii) were isolated already on an island or peninsula large enough to permit persistence of a population or iii) were widespread on West Antarctica before its breakup began in the Oligocene (Katz, 1982).

The status of the junction between Australia and East Antarctica at and prior to the time of the sea floor spreading in the Paleocene is as follows.

Falvey (1974) develops an explanation of the events associated with passive fracturing of continental plates. First, there is an uplift due to thermal expansion. This is followed by subsidence caused by metamorphism in the deep crust. On the surface these can be seen as three phases: prerift, rift valley and post-breakup. Falvey visualizes that the first phase occurred possibly 50 million years before breakup.

A drill hole sequence in the Eyre sub-basin south of Australia suggests that the Australian-Antarctic fracture zone could have been in existence at least since Middle Jurassic (Bein & Taylor, 1981).

Lakes were widespread in Australia during the Jurassic (Coleman, 1980) and these were followed by marine transgressions in the Early and middle Cretaceous which effectively divided Australia into a number of islands (Morgan, 1980). This is consistent with the model developed by Falvey (1974). Hallam (1981) has emphasized the world-wide occurrence of eustacy at this time. These marine transgressions ended in Australia by the Late Cretaceous (Deighton *et al.*, 1976). There is no certainty, however, as to the last time any part of the Australia-Antarctic rift was above sea level.

In the Paleocene, the separation of Australia and Antarctica was by means of a more or less narrow strait, narrowest adjacent to Cape Leeuwin, Western Australia (Crook, 1981). Notably in this connection, the present shelf between the shore and the 2 km isobath (taken as the continental edge) is greater than 50 km and may represent the sea-covered continental margin at the time of rifting.

The revised identification of the magnetic anomalies south of Australia by Cande & Mutter (1982) yields an interpretation of the break-up of Australia/Antarctica as being between 90 and 110 mybp. This interpretation gives validity to the reasoning developed above. It suggests, moreover, that an over-water, rather than overland, route was taken by those organisms which evolved in the late Mesozoic and entered Australia in the Late Cretaceous or early Tertiary.

When faunal movement was possible between America and Australia by way of the Antarctic Peninsula, West Antarctica and East Antarctica, the land to be traversed by migrants or colonists would be at high latitudes. Even though temperatures were higher and ice was absent (Thompson & Burn, 1977), if the obliquity of the ecliptic was then as it is now,

these latitudes would be subject to short winter days. Douglas & Williams (1982) point out that the Antarctic flora at this time shows little evidence of such an influence.

The elements of floral composition and high latitudes may have acted as a filter device. Vegetation dominated by gymnosperms and *Nothofagus* may have been satisfactory for small insectivores or omnivores, but unsuited to eutherian herbivores.

In summary, when considering the Gondwanan connections, particularly the Australian, Antarctic and South American breakup of Gondwana as a dispersal route, the following constraints need to be kept in mind:

1. The nature of the South American-Antarctic Peninsula connection now is believed to be tectonically more active and more complex than previously held.
2. The Drake Passage began to open about 29 mybp and was sufficient size by 23.5±2.5 mybp for the development of the South Circumpolar Current.
3. Terrestrial bird tracks of Oligocene/Miocene have been identified south of Drake Passage.
4. West Antarctica is now an archipelago, but the faulting is possibly of Oligocene age.
5. The Australian-East Antarctic separation in the Paleocene was along a fracture zone and rift valley of at least Jurassic and possibly Paleozoic age.
6. During the Cretaceous, there were extensive marine transgressions over Australia so that it was reduced to a number of islands. Presumably, similar transgressions occurred in East Antarctica. The marine transgressions receded in the Late Cretaceous.
7. At the time that seafloor spreading commenced, the size of the rift valley and the nature of the sea between what is taken as the Australian continental boundary and the shore line are unknown.
8. The high latitudes of the possible migration route, the nature of the vegetation and the extended lake systems which may have followed the recession of the marine transgressions, are likely to have restricted the passage of many potential colonists of Australia from South America.

Connections: Australia, Asia: A consequence of the movement of the Australian Plate is the long isolation which allowed the autochthonous faunal elements to evolve.

Whether there were any transient faunal connections to the north when rare invasions of animals occurred before the Australian Plate finally joined with Asia in mid-Miocene times needs to be addressed. Audley-Charles *et al.* (1981), Coleman (1980) and Powell *et al.* (1981) have discussed the geological changes which occurred to the north of Australia as it approached Asia. Clearly, it was not a simple collision. All the above offer plate tectonic explanations of Wallace's and Weber's lines and, thus, insights into the boundaries of Asian and Australian faunal distributions. Cranbrook (1981), however, in discussing the fauna in the vicinity of Wallace's and Weber's lines, points out that some faunal elements do transgress these boundaries and that the transgressions are marked when fossil occurrences such as that of the proboscidian *Stegodon* on Timor and Flores are taken into account. Cranbrook (1981) interprets the unbalanced fauna as evidence of over-water dispersal. The faunal breaks between the Asian and Australian plates are interpreted as being related to climatic effects which induced faunal changes in a seasonally arid region lying between wetter and less seasonal areas to the west and east.

While Australia was moving northward, India also was moving, but their relative positions have not changed during the past 50 million years (Norton, 1982). A water gap would have existed between India and Australia at all times from late Mesozoic, so any dispersal would have been over water.

Deep sea cores along the Ninety East Ridge yield pollen reflecting island floras of Paleocene and Oligocene ages. These show primary similarities to the early Tertiary floras of Australia and New Zealand. Although these islands were then closer to southern land masses, Kemp & Harris (1975) interpret their colonization as occurring through long distance dispersal mechanisms. Whether any fauna, especially invertebrates, were interchanged between Gondwanan fragments during the above events is not known. Crawford (1974) explains the distribution of *Daphniopsis* in Australia, Kerguelen, Tibet and Mongolia as reflecting its occurrence on islands of the Ninety East Ridge and fragments of Gondwana which include Tarim, Tibet and north China (see also Lin *et al.*, 1985). A similar rafting of acanthodriline oligochaete fauna may have resulted in the similarities noted by Jamieson (1981) between India and Australia.

McKenna (1973) discusses all the various types of dispersal routes under the headings of sweepstakes, filters, corridors, Noah's Arks and beached Viking ships. His conclusion is that while Matthews' and Simpson's principles of palaeobiology were conceived within a stable continental framework, they are in fact compatible with plate tectonic synthesis. The principles also can be extended to include a type of organic dispersal (Noah's Arks, for example India, Australia) and the transfer of fossils from one land mass to another (beached Viking ships, for example India, the fossil myobatrachid frog *Indobatrachus*).

McKenna (1973) tabulates the principal Cainozoic corridors, sweepstakes, filters and arks under a plate tectonic rationale. Those relevant to this analysis are his: corridor - East Antarctica/Australia earliest Cainozoic; filters - within-continent examples for Australia would be extensive lake systems in the early Cainozoic and dune fields in the later Cainozoic and during Pleistocene climatic oscillations; sweepstakes - Australia/Antarctica in early Cainozoic, Australia/Asia in late Cainozoic; and arks - Australia now docking with Asia and India docking with Asia in the Cainozoic.

Summary: The foregoing indicates that despite a very great increase in knowledge of the past distribution of land on the earth's surface there is still no certainty of the precise environmental conditions associated with fragmentation and suturing of continental Australia.

Despite the imponderables, the fauna of Australia speculatively consists of elements:

- (a) persisting since Australia was part of a large supercontinent;
- (b) derived by overland dispersal from other land masses, for example South America after the supercontinent had lost some fragments;
- (c) dispersed over archipelagos or islands as Australia broke from Antarctica or sutured to Asia;
- (d) evolved in Australia while it was fragmented by a eustatic rise during the Cretaceous;
- (e) resulting from chance long-distance overseas dispersal;
- (f) introduced by man.

In the light of the constraints on interpretation imposed by geology, the following Section sets out what possible criteria might be used to identify these elements.

Examples

Introductions by Man: This is a most heterogeneous group, dealt with in detail in Chapter 10 of this Volume.

The broad ecological characteristic of inadvertent introductions is that they generally are restricted to areas occupied by or disturbed by human settlement. When established, they are common, very abundant and tend to be pests. Frequently, the precise conditions associated with their arrival are unknown, but because of their nuisance or pest status their presence is well documented. The original distribution of many species is well known and, in some cases, their spread throughout the world is documented, for example the Argentine Ant *Iridomyrmex humilis*. Nevertheless, the precise place of origin of many Australian colonists is frequently doubtful, for example the so-called peregrine species such as earthworms or the "tramp" species of ants. Such uncertainty does not hold for deliberate introductions made in the cause of biological control.

Many populations of introduced species are of interest as evolutionary studies because of the genetic responses to control measures.

Indigenous fauna: This section deals with the present distribution of animals and their possible origins in the light of two current hypotheses used to interpret observed distributions: those in which dispersal is possible and those in which vicariance is taken as the principal factor. Darlington (1957; 1965; 1971), Matthews (1939), Mayr (1972) and Simpson (1961) saw patterns when new faunal elements arose in one region and then apparently dispersed or expanded their ranges into more distant parts. Such patterns are conspicuous in the case of mammals and birds. The interpretations of these workers have been supported by McKenna (1973) who extended this dispersal model so that it is compatible with plate tectonic synthesis.

The problem of origins and dispersal has been stated in the context of stasis, large wide-ranging species which persist with very little change and without giving rise to novelties for a long time and punctuated evolution when new or novel forms appear in the fossil record which cannot readily be seen to be descendants of the persistent static species (Eldridge, 1971; Eldridge & Gould, 1972). The essence of this interpretation is that novel forms do not appear to arise by slow evolution from a persistent form or species. Either they arise from small isolated populations, leaving no fossil record, or by a process different from that occurring in widespread persistent forms. Whatever their mode of origin, novelties become widespread only through dispersal.

Dispersal phenomena have been used most recently in a theoretical framework by MacArthur & Wilson (1967) in a study of island biogeography. The presence and position of epicontinental seas are of immense significance for biogeographic interpretations. Theories using only movement of continental plates to explain disjunct relationships are too simplistic (Howden, 1974). Howden (1977) documents the arrival, following a stormy period, on an Australian eastern coast beach of beetles of families known from Hawaii and Samoa. These findings demonstrate the significance of over-water dispersal in understanding island biogeography.

Thornton (1983) points out that when animals known to be good and poor dispersers are found together, it presumes an origin by way of vicariance. If only good dispersers are present, dispersal is suggested.

In contrast to the foregoing, those biogeographers favouring an interpretation of distribution based on vicariance see patterns in which wide spread faunal elements are shown to be common to many areas. Should these be shown to occur or

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to be part of a once larger continuous land mass, then the common faunal elements are taken to be part of a former once cosmopolitan fauna (Croizat *et al.*, 1974).

Possible dispersal is conceded, but identified only for elements which do not conform to the cosmopolitan pattern or where sympatry occurs. This last follows because speciation is allopatric, resulting from a vicariance event. Sympatry must reflect dispersal.

From the above it is possible to say:

1. Any faunal element which has a fossil history indicating an age older than the period when Australia first was completely isolated could have entered the continent by a southern route or been part of the fauna of Pangaea or of a former southern continent.
2. Any faunal element which has a fossil record or, in evolutionary terms, is younger than Australia's isolation in the south could have reached the continent across a water gap, initially from the south, later from the north.
3. Some elements entering from the north could have been derived from elements rafted to Asia by drifting continental crust such as greater India, thus showing northern origins, but southern affinities (Noah's Arks in McKenna's (1973) terminology).
4. The significance of Sundaland in permitting Palaeoarctic elements to enter Australia is difficult to assess, but the youthfulness of some Asian faunal elements is difficult to reconcile with an early arrival.
5. Faunal elements which were widespread in greater Gondwana before it was fragmented by the loss of Africa in the Cretaceous might, in theory, still persist. Such an occurrence might be indicated by faunal relationships between all southern plates or between Australia and the plates which were first to leave Gondwana. Examples would be *Heleophryne* if it is a leptodactylid frog, all Onychophora, Migidae (mygalomorph spiders), lungfish and ratite birds.

A choice in interpretations of faunal origins lies between one based on the assumption that the geological evidence is good enough to support an hypothesis of dispersal over dry land, or one which interprets the geological evidence, though not the dates of sea floor spreading, as inadequate for decision. There may be cases of vicariance and dispersal among the faunal elements showing southern affinities. The caution expressed by Kirsch (1984a) that many geological patterns can be consistent with particular cladograms would appear to be warranted. It is impossible to say unambiguously that elements did not arrive by island hopping, but it should be considered a possibility in view of the South American organisms not found in Australia. Some sort of filter or sweepstake route would be consistent with the geological evidence.

When biogeographers, using the vicariance methodology coupled with cladistic analysis of the common faunal elements, show congruence of biological and area cladograms, congruence is interpreted to indicate that specified events of palaeogeography can be adopted as explanations of biological patterns. A decision concerning the nature of this correspondence (vicariance, dispersal or a combination) is related to the parsimony of the explanation (Platnick & Nelson, 1978; Rosen, 1978; Nelson, 1973; Nelson & Platnick, 1981).

Not all the faunal elements with apparent affinities to the fauna of other southern land masses have been analysed by the above methodology nor in equal detail. The southern faunal element in Australia, however, could include: gnaphosid spiders of the genus *Eilica* (Platnick, 1976); snails of the genus *Bothriembryon*; trap-door spiders of the families Actinopodidae and Migidae; peloridiid Homoptera (China,

1962); labinine ichneumonids (Gauld, 1983); hylid frogs (Tyler, 1984; Maxson & Wilson, 1975); leptodactylid frogs (Lynch, 1971); side-necked turtles (Gaffney, 1977); ratite birds (Cracraft, 1974; Sibley & Ahlquist, 1981; Stapel *et al.*, 1984), but see Rich & Balouet (1984); non-passeriform birds (Rich, 1975); and marsupials (Archer, 1984; Kirsch, 1984b).

Diplodactyline geckos are restricted to Australia and nearby islands. Kluge (1967a) accepts their derivation from a stock related to Jurassic fossils. Moreover, the lizard family Pygopodidae, closely related to geckos (Underwood, 1957), also could be so derived. Interpretation in this way of age and affinities from fossil evidence would suggest that these autochthonous elements are derived from Pangaeanic elements isolated by the fracturing of Gondwana.

There are many autochthonous groups which, unlike the geckos, lack a fossil history yet are of an antiquity that allows for the possibility that they are survivors of an old Pangaeanic element or part of a regional fauna of Gondwana. Termites, which are Mesozoic insects (Gay & Calaby, 1970), could provide examples. *Mastotermes*, a primitive and typical Australian termite, is known from the Tertiary of the Northern Hemisphere. *Valditermes* is a fossil damp wood termite from the Early Cretaceous of England (Jarzemowski, 1981). While the southern damp wood genus *Stolotermes*, with species from Australia, New Zealand and South Africa, could be interpreted as a southern faunal element, there is the possibility that it represents a Pangaeanic or regional Gondwanan element.

Darlington (1957) raises the questions whether pigeons (Columbidae) or parrots (Psittacidae) could have arisen in the Australian region, where they are most numerous. He dismisses this possibility because these old groups likely have had a complex history and are now declining in dominance. The possibility that these elements are an autochthonous element needs re-examination (Rich, 1975).

The opportunity for faunal interchange arose as soon as Australia collided with Asia. In the absence of geological knowledge, the order in which Australian fauna with Asian affinities arrived can be inferred from the taxonomic rank of the faunal elements. Thus, conspecifics distributed between Asia and Australia are regarded as recent entrants. Asian genera with Australian species are considered to be later arrivals and higher taxa are even older. (This is the methodology of Mayr, 1944; Darlington, 1957; 1971; Rich, 1975). Nelson (1974) specifically rejects this method as a possible guide with respect to vicariance events. He interprets discrepancies in rank as evidence of different rates of evolution and not temporally different origins. Different rates of evolution are always likely, but as Australia sutured to Asia, chance dispersal over the intervening archipelago became increasingly likely. In this context and the absence of fossils, taxonomic rank becomes a guide to age of entry.

Bats (Chiroptera) are distributed widely. There are two endemic Australian genera (*Macroderma* and *Rhinonycteris*). There are Australian fossil bats of Miocene age (Archer, 1978). Hand (1985) has identified a megadermatid from the Miocene and discusses two possibilities: that megadermatids are essentially an Australian stock or, alternatively, dispersed into Australia.

Rodents have been found as fossils of Pliocene age and presumably entered Australia between four and five million years ago (Archer, 1981). This suggests their late arrival with respect to the junction of Australia with Asia.

Simpson (1961) divides the Australian rodents as follows: the local members of the wide spread *Rattus*, old Papuan genera two of which occur in Australia (*Uromys* and *Melomys*), the *Pseudomys* group and the sub-family Hydromyinae. Lee *et al.* (1981) and Baverstock (1984), however, interpret

karyological data to indicate that Australian rodents, with the exception of *Rattus*, are a radiation of a monophyletic stock which arrived relatively late in geological time. If true, this late arrival indicates constraints on access to or the nature of the sweepstake route available immediately following the suturing of Australia to Asia in the Miocene. Baverstock (1984), however, points out that the molecular distinctness observed among Australian rodents normally would be expected to take 10 to 15 million years to develop. Alternatively, molecular evolution may have been more rapid than in other mammals or extra-Australian diversification took place earlier, followed by invasion as a partly differentiated stock (Baverstock, 1984). Clarification of these alternatives requires a similar study of the rodents of Indonesia.

Birds are the group within which relationships to Asia and postulated time of entry to Australia most often have been deduced from taxonomic affinities. Mayr (1944) recognizes the following: a recent group in which only subspecific distinction is recognized; a group which has diverged at the specific level and assumed to be of Pleistocene or Pliocene age; a group of genera endemic to Australia and Papua, but with clear relationships to Asiatic genera which are interpreted as either Pliocene or Miocene migrants; another group of greater age is composed of subfamilies and families which are interpreted as having reached Australia during the early or middle Tertiary, but clearly related to old world families; and finally, a group of very old endemic families whose affinities are uncertain. This last group includes the ratites *Dromaius* and *Casuarius* and megapodes *Leipoa*, *Megapodius* and *Alectura* among others. Serventy (1972) reviews possible origins in the light of continental drift.

Recently, biochemical and molecular techniques have been used to study phylogenetic relationships of birds (Sibley, 1970; Sibley & Ahlquist, 1981; 1985). Sibley & Ahlquist (1981) suggest that ratites are a homogeneous group and that of the passerines, suboscines and oscines are unrelated (Sibley & Ahlquist, 1985). Two suborders of Passeriformes, the Oligomyodi for the suboscines and Passere for the oscines, are recognized. *Pitta* is the representative of the Oligomyodi in Australia and presumed to be a recent arrival. In the Passeres, the two parvorders Corvi and Muscicapae are recognized and the large family "Muscicapidae" is seen as a polyphyletic assemblage. The Corvi is interpreted as having originated in Australia and radiated in isolation during the Tertiary. Ancestors of the Corvini (crows and jays) were able to disperse to Asia in the middle Tertiary where they underwent a Holarctic radiation. The Australian species of *Corvus* are presumed to be descendants of recent immigrants from Asia (Sibley & Ahlquist, 1985).

These findings emphasize the significance of Australia as an isolate and centre of evolution as it drifted north during early Tertiary times. Corvi should appear alongside agamippine trap-door spiders, heptialid moths, hylid and myobatrachid frogs, diplodactyline geckos, pygopodids and marsupials as examples of outstanding radiations.

The origin of the reptile families Agamidae, Scincidae, Varanidae, Elapidae and non-diplodactyline geckos is generally agreed to be Asian (Cogger & Heatwole, 1981). They are believed to have arrived in Australia from early Tertiary to Pleistocene. There were possibly several migrations of the agamids, with *Moloch* representing the first. There have been radiations in all groups, however, and better knowledge of scincid phylogenetic relationships in particular is required before any certainty can be attributed to interpretations of arrival time and subsequent evolution.

The insects are a very old group and in some cases the same genera are known from Mesozoic fossils. Insects also exhibit such diversity that their biogeographic and phylogenetic relationships can be known only to specialists until taxonomic

reviews are compiled. Because of their age, however, southern autochthonous and sweepstake elements in the Australian fauna are to be expected.

Tindale (1981) suggests that the Lepidoptera (butterflies and moths) had an origin in the early Mesozoic and that the now relict distributions of some archaic groups might predate the break-up of Pangaea. He also suggests that the remarkable diversity of the Hepialidae in Australia argues that they have had a very long history on the continent. Some of the archaic groups show southern relationships, but there has been much colonization of Australia from the north indicating significant ability to cross water gaps.

Howden (1981) points out that 100 Australian genera of Coleoptera (beetles) have worldwide distributions. These fall into two groups: one possibly old (Jurassic-Cretaceous), for example *Cupes*, and another Tertiary, for example *Cicindella*. The now cosmopolitan genus *Onthophagus* (Scarabaeinae) is represented in Australia by 150 species (Howden, 1981). The interpretation of Matthews (1972) is that this group has been established by as many as 34 separate invasions. Matthews (1976), discusses scarabaeine dung beetles of Australia (Tribe Coprini) and sees elements derived at remote times from the north as well as some from Africa.

Species of Ichneumonidae (parasitic wasps) are known from fossils from the Late Cretaceous and may have arisen earlier (Gauld, 1984). Of the Ophioninae, which are parasites of lepidopterous larvae, some such as *Xylophion* and *Riekophion* are endemics. There are other genera with southern relationships and some disjunct species groups with Malayan/Asian affinities.

Brown (1973) interprets the evolution and distribution of the Formicidae (ants) in the classical Darlingtonian framework. Evolution of the advanced forms took place in Eurasia, expanding and pushing the primitive forms to the periphery. He interprets the Australian ant fauna as being a primitive (for example *Nothomyrmecia macrops*) but varied fauna with many endemic genera which radiated into drier vegetation zones. This implies a long evolution within Australia.

Among the Mygalomorphae or trap door-spiders, *Conothelae* (Ctenizidae) occurs from Asia to Australia. The young spiders are dispersed on gossamer. *Conothelae* is never abundant, but is widespread in arid Australia. The families Theraphosidae and Barychelidae are distributed widely outside Australia. In Australia, there are endemic genera which have an essentially tropical distribution, but are common in arid habitats.

Many araneomorph spider families are cosmopolitan, but species of *Nephila* and *Cyrtophora* range from Indonesia to Australia and Polynesia.

Australia is the only continent on which endemic terrestrial members of the Nemertina (ribbon worms) occur. Elsewhere, these are found only on islands where parallel evolution from marine ancestors is believed to have occurred consequent upon the eustatic rises and falls during the Pleistocene (Moore & Gibson 1981; Moore, 1985). *Argonemertes*, the Australian genus, is found in southwestern and southeastern Australia. If empty island habitats are a prerequisite for successful terrestrial invasion, then *Argonemertes* may be a relict from the Cretaceous when Australia, as a result of the widespread epicontinent seas of that time, was an archipelago.

ADAPTATIONS

Introduced Fauna

The introduced species which have become pests have been subject to either chemical, biological or integrated control measures. In effect, these attempts to eliminate, regulate or reduce numerically are changes of considerable magnitude to the environment of the target species. The responses of the pest populations represent examples of adaptive evolution. Development of resistance to insecticides is a common occurrence. Some organisms, however, evolved resistance to control chemicals before the introduction of modern insecticides. The Cattle Tick, *Boophilus microplus*, is a pest of cattle in Queensland and northern Australia. It was controlled by an arsenical dip until 1936, when failure of control and resistance were first recorded. Use of increased concentrations of arsenic was not possible because of its effect on the skin of cattle (Anon., 1978; Hart, 1982). DDT and other organochlorines were introduced for tick control in 1945 and by 1962 DDT resistance was apparent. In 1962, organochlorines were banned from use in cattle dips because of unacceptably high residues in meat.

Organophosphates (OP) were used next, but resistance to this class of acaricide appeared by 1963. By the 1980's there were 13 resistant strains of *Boophilus microplus* in Queensland, having at that time in various localities reduced the efficacy of 17 of the 19 different acaricides registered for use. Eight of these strains are resistant to OP. Their responses are determined by enzyme changes resulting from different resistance (R) genes. The inheritance of R genes appears to be as follows: OP resistance incompletely dominant, DDT incompletely recessive and dieldrin completely dominant. The resistance shown by some strains, such as Ridgelands and Biara, are thought to be due to insensitive brain acetylcholinesterase (AChE), but others, like the Mackay strain, have a detoxifying enzyme (Hart, 1982). Some strains resistant to DDT have been shown to be resistant to synthetic pyrethroids (Nolan *et al.*, 1977). Synthetic pyrethroids can have their effect enhanced by the simultaneous use of OP acaricides.

A further development has been the use of amidine tickicides. In some cases these cause the larval ticks to fall off the host. A strain has now developed, however, which is resistant to three amidine tickicides. This resistance is thought to be due to the altered sensitivity of the target rather than to the metabolism of the tickicides (Nolan, 1981).

The control of *Boophilus microplus* illustrates the diverse response of different populations of the same organism to a sustained high level of selection. Resistance may be due to one or a combination of the following: change in the permeability of the integument, change in sensitivity of the target organism and selection of enzymes which detoxify the insecticide. In the face of sustained application of insecticides, mutations of genes which endow the target organism with any of these attributes are selected quickly and spread through the population. Different strains of *B. microplus* appear to have arisen independently as the result of selection for the different genetic factors which endow them with resistance (Hart, 1982). The resistance of *B. microplus* shows that there is neither a single solution nor a single pathway in the evolution of resistance.

Because of its importance to the sheep industry, the Australian Sheep Blowfly, *Lucilia cuprina*, has long been subject to control. The development of resistance to a number of insecticides has led to a detailed genetic study of their nature and genetic control. After the introduction in 1955 of dieldrin as the major insecticide, resistance appeared and was widespread

in field populations after two seasons (Whitten *et al.*, 1975). This was due to the spread of a single gene (Rdl) on chromosome 5. Since the cessation of the use of dieldrin, control has been by organophosphorus insecticides. Dieldrin resistant genes are still present, however, in the population 24 years after dieldrin was widely used (Hart, 1982). In studies of the Rdl locus, Whitten *et al.* (1980) found strong support for selection during development of larvae in fleeces of sheep containing insecticide residues. They also found that the resistant genotype appears to be at a disadvantage both in the laboratory and in the insecticide-free control sheep.

The OP resistance in *Lucilia* is carried at a locus on chromosome 4 and another on chromosome 6. The former locus has four alleles, wild-type or susceptible, Rop-1A, Rop-1B and Rop-1C. The latter locus, Rop-2, exists in two allelic states, wild-type and resistant. Rop-1C is known only from the laboratory and has not been found in the field (Hart, 1982). When Rop-1 alleles are heterozygous, their effects are additive. Rop-1 and Rop-2 alleles, however, are multiplicative (Whitten *et al.*, 1975). There is apparently no difference in penetration between the resistant or susceptible strains of *L. cuprina*. Nor was there any difference between these strains in the sensitivity of head acetylcholinesterase or target enzyme of OP's. Both susceptible and resistant *L. cuprina* appear to detoxify OP's via a number of pathways, but the resistant strains produce more of the metabolites (Hart, 1982).

McKenzie *et al.* (1982) followed up the observation that the diazinon resistant gene was not now at a disadvantage as 10 years previously. In laboratory and field studies, they showed that resistant and susceptible diazinon genotypes may have similar fitness in environments free of diazinon. If the genetic background of field animals is disrupted, however, then fitness of the resistant genotype declines. These results were interpreted to indicate that there had been a modification of the genetic background in field populations since the spread of the resistant allele some 10 years earlier. McKenzie *et al.* (1982) suggest that the outcome resulted from genetic variability, the intensity of selection and the duration of insecticide usage after resistance developed. These examples show that populations, in the face of sustained and intense selection by way of novel environmental factors, are capable of evolving genotypes and phenotypes which can develop and multiply even with high initial mortality. These examples are not unique and the phenomenon of evolved resistance to chemical control agents is widespread, ranging from nematodes to a very large array of arthropods and rodents.

A more complex evolutionary response was forthcoming when biological control was used to regulate the populations of the Rabbit, *Oryctolagus cuniculus*, by use of the disease myxomatosis. At the beginning of the control campaign a virulent strain of myxoma virus was used. Mosquitoes serve as mechanical vectors. Transmission depends upon the presence of sufficient viral particles on the proboscis to inoculate a new host when a mosquito takes its next meal. Such a mechanism is most successful when there are high levels of viral particles circulating for long periods in the blood of animals which act as reservoirs of infection.

The initial strains of myxoma caused sickness and death very quickly. The first outbreak had a mortality of 99.8%. By the next season mortality had fallen to 90% (Fenner, 1983). The myxoma-induced mortality selected against virulent strains of virus because they had briefer periods of access to vectors compared with less virulent longer acting strains. Moreover, the less intense mortality caused by the virulent strains in the second season meant that selection for rabbits resistant to the virus could proceed in a way analogous to the application of chemical insecticides. The result was that moderately virulent strains became dominant and remained so despite the repeated introduction of more virulent strains. The mortality

induced in rabbits fell from 90% to 50% or below and this was accompanied by changes in clinical severity. The end of the coevolution in the short term is that a moderately virulent grade of virus becomes established in rabbit populations in which some genetic resistance has developed.

In terms of the older literature, the variability in the permeability of the integument, the sensitivity of the target organs or the presence and variability of generalized or specific detoxifying enzymes are to be considered preadaptations in *Boophilus microplus* and *Lucilia cuprina* for insecticide resistance. Gould & Vrba (1982), however, would argue that these abilities are adaptations to deleterious substances which may occur in the normal environment of the organisms, but not in anticipation of the future presence of chlorinated hydrocarbons, organophosphates or amidine acaricides. Gould & Vrba (1982) would regard such metabolic capacities that now enhance fitness, but were not built by natural selection for their current role, as exaptation. Thus, the integument of arthropods, the target organs such as the central nervous system and the various systems of detoxifying enzymes are to be regarded as a unified system of adaptation to harmful or deleterious substances which may occur from time to time in the environment of the organism. Where these adaptive responses become coopted to their new role in resisting novel but specific toxic chemicals, they are to be regarded as exaptations. Because of their former adaptive nature, these attributes are to be considered preadaptations rather than preadaptations to the new chemicals present in the environment as a result of man's desire to regulate pest arthropods.

The very complicated geographic and climatic history of the Australian continent since the Cretaceous means that there have been many opportunities for the fauna to take functions that arose as adaptations for one purpose and coopt them for another purpose. Should this be so, recognizing or distinguishing the order in which adaptive responses occurred in the fauna is as important as attributing a present-day function. The earlier the initial adaptive response occurred, the more difficult it will be to disentangle initial causes from subsequent elaborations of the response.

Indigenous Fauna

Selection and adaptive responses of the indigenous fauna are known in only broad outline compared with the detail known for introduced fauna. Nevertheless, responses which are clearly adaptive can be recognized. These range from ability to eat toxic substances or material that is difficult to digest to responses to the aridity or unpredictability of the present environment. The problem is not so much to describe adaptive structures, functions or behaviour, but to recognize their origins and history.

In the case of native animals whose adaptations are of long standing, it is not possible to study the way the adaptations arose as was done in the examples of introduced fauna. Adaptations can be established, however, by making comparisons: between the same populations at different times (insecticide resistance); between populations of the same species (the different examples of resistance in populations of *Boophilus microplus*); between species of the same genus occupying contrasting environments or between less closely related groups. Nevertheless, all statements about adaptation are relative to some base, the consequence of a judgement following a comparison (Main & Bakker, 1981).

The adaptations may be to toxic substances, quality of food, heat or cold, shortage of water, or to other organisms in the environment. The selective forces may be operating now or have only operated in the past (dieldrin in case of *Lucilia*). They may affect only part of a con-specific population or the

whole population. The elucidation of causes of adaptive responses can proceed most readily when the causes operate now, but only affect part of a population. Association of cause and effect is much more difficult if the whole population is affected and the trait arose in the distant past. This is adaptation and preadaptation or the adaptation and exaptation of Gould & Vrba (1982).

There are many species of toxic plants in Australia. A most spectacular example of tolerance to toxic substances is found among those species of herbivores whose range overlaps that of the toxic plant species of the genera *Gastrolobium* and *Oxylobium*. The toxic species of these genera for the most part are found in the southwest of Western Australia (Aplin, 1971). They are legumes growing as perennial shrubs and so available as dietary items for long periods. The toxic principle is sodium fluoroacetate, commonly known as the commercial poison 1080. The metabolite, fluoroacetic acid, blocks the Krebs Cycle at the citrate stage and so interferes with energy metabolism.

The question of tolerance or resistance to poisons by field populations of wild animals normally would arise only if animals were seen or known to eat (by analysis of faeces or stomach contents for plant epidermis) the toxic plant. In the case of tolerance to 1080, the information only came to light when the commercial preparation was to be used to control rabbit numbers without endangering native animals.

Test results (Oliver *et al.*, 1977; King *et al.*, 1978) indicated that there were different susceptibilities in conspecifics (*Rattus fuscipes* and *Trichosurus vulpecula*) populations from inside and outside the ranges of fluoracetate bearing plants. Animals from inside the range of the toxic plants were highly resistant to sodium fluoroacetate, while those from outside were very intolerant and showed signs of poisoning at much lower levels of poison. Also, *Macropus fuliginosus*, whose range includes that of poison plants, had a greater tolerance than *Macropus rufus* whose range is outside that of the sodium fluoroacetate bearing plant species. Other species occupying ranges containing poison plants also show similar tolerances or resistance to poisoning such as *Setonix brachyurus* (Mead *et al.*, 1985).

These findings are consistent with an interpretation that the differences represent adaptive responses to the presence of sodium fluoroacetate in food plants. The basis of the tolerance seems to be analogous to the cases of insecticide resistance already discussed.

The macropodid marsupials (kangaroos and wallabies) are well known as the dominant mammalian herbivores in Australia. In many respects, including their ability to digest fibrous diets, they are the analogue of ruminants elsewhere and have been referred to as ruminant-like. Because many domestic animals are ruminants and able, with the aid of the bacterial gut flora of the rumen, to digest an otherwise refractory fibrous diet, the nutrition of ruminants has interested agricultural scientists and veterinarians. Following the demonstration that kangaroos and wallabies could digest fibrous diet and, like ruminants, are able to recycle urea to the gut (Brown 1968; Brown & Main, 1967) and do so in the field (Kinnear & Main, 1975), this ability is construed as an adaptation on the part of kangaroos to the high fibre, low protein plants which are ubiquitous in Australia (Hume, 1982).

The ability to handle low quality high fibre diets is an adaptive advantage in kangaroos. Whether the adaptation arose particularly in response to the fibrous diet, *per se*, is not clear. Rat-kangaroos (*Bettongia* spp.), whose diet is not highly fibrous, have an enlarged "forestomach" within which food is retained and fermented. Study of the diet of *Bettongia penicillata* reveals that underground fungi are frequent dietary items. Analysis of these fungi shows that while they

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appear to be adequate as a total nitrogen source, the amino acid composition is unbalanced completely and, in this sense, quite inadequate. Following fermentation in the "forestomach", however, the amino acid composition becomes balanced with respect to normal dietary requirements (Kinnear *et al.*, 1979).

The response of *Bettongia* spp. to a dietary inadequacy in the form of unbalanced fungal amino acid has been to retain the food and ferment it by bacteria within a sacculated part of the foregut; the bacterial cells and the fermentation product are digested later. Kinnear & Main (1979) interpret this as an adaptive response which enables diet and nutritional needs to be matched and as a preadaptation from which the more elaborate ruminant-like digestion of kangaroos could evolve. In the terminology of Gould & Vrba (1982), it is an adaptation which has been coopted to the function of handling a fibrous diet; the ability of kangaroos to handle fibre is an exaptation.

The predominance of hot, dry and unpredictable seasonal climates in Australia has selected all groups of animals for adaptive responses to these potential causes of death. The adaptations range from inconspicuous behavioural traits to marked morphological changes. Genetically, this ranges from the readily reversible (little genetic commitment), through those adaptations in which genetic commitment is not complete (some variability and altered response in a changed environment is still possible), to those whose genetic commitment is complete and the process is irreversible. Such an example is the completely integrated developmental, morphological and physiological response of kangaroos.

Many of the studies of adaptive responses of Australian terrestrial animals to conditions of lack of water and high temperatures have been concerned with extremes which can be tolerated. Extreme conditions are avoided wherever possible, generally by behavioural means. The commonness (Fisher *et al.*, 1972) of activity during the cooler parts of the day as with birds, nocturnal activity as is the case with most marsupials, activities during cooler, moister seasons as in the burrowing frogs *Neobatrachus*, *Heleioporus* and *Cyclorana* (Main, 1968; van Beurden, 1982) or the dispersion of young and mating of adult mygalomorph spiders in cool or damp seasons (Main, 1982), attests to the efficacy of behaviour as an adaptive response for avoiding harmful conditions.

While laboratory experiments preclude behavioural responses, the results frequently show marked differences between species in their capacity to withstand dryness and heat (Licht *et al.*, 1966a). In general, these responses relate in such a way to the habitats occupied and the risks faced that the ability to endure high temperature is an adaptive trait. Notwithstanding a demonstrable ability to resist high temperatures, most species of lizards in the field show a marked behavioural response which ensures that a preferred body temperature is maintained (Licht *et al.*, 1966b; Bradshaw & Main, 1968; Heatwole, 1970). The efficacy of behaviour as a labile adaptive response should not be overlooked or discounted.

Polymorphism offers an example of genetic commitment to the production of adaptive phenotypes. Studies of adaptive responses by way of polymorphism are few. The frog *Crinia pseudinsignifera* is, like other species of the genus, polymorphic for back pattern. The pattern is inherited in a simple Mendelian manner. The abundance of the dominant trait correlates with continentality of the location; on a geographic scale it increases in frequency in step with the decrease in the mean nightly minimum temperature during the breeding season. At the extreme inland limit of the species the recessive homozygote is absent and only one phenotype occurs (Main, 1968 and unpubl.).

Another example which appears to have a genetic basis is found in the brightly coloured araneomorph spider *Gasteracantha minax*. In southern populations of this species a completely melanic form occurs with a variable frequency in cool, cloudy localities and is more abundant in cool seasons (B.Y. Main, pers. obs.). The melanic presumably has an advantage over normal with respect to maintaining high body temperature by absorbing solar radiation. The inheritance of the melanic form has not been studied, but the system is likely a simple one.

A further example suggestive of a genetic mechanism is that of the agamid lizard *Amphibolurus ornatus*. Two types of juvenile are present, one classed as fast growing, the other slow growing. The fast growing juveniles survive better in winters when frequency of frosts was high, but poorly during the hot dry summer. Slow growing animals show the converse response (Bradshaw, 1971).

These examples suggest that adaptive responses which are genetically controlled polymorphisms may be relatively common.

Further investigations may reveal examples among the following: heat tolerance and water economy among the species of Australian chats of the genus *Epthianura* (Williams & Main, 1976; 1977) and parrots of the genus *Neophema* (Lindgren, 1973), among macropodids (Brown & Main, 1967; Brown, 1968), lizards (Bradshaw, 1970), mygalomorph spiders (Gray, 1968) or lycosid spiders (Lane, 1965).

In all these cases where differences are apparent there is, with few exceptions, a correlation between ability to tolerate high temperature with good water economy and occupancy of hot dry habitats. In a general way, species occupying inland ranges have better tolerances of high temperatures and better water economies than congeners which occupy peripheral ranges.

The physiological mechanisms involved range from reduced metabolic needs in kangaroos and wallabies (Brown, 1968), increased efficiency at handling water losses (see Dawson, 1981 for review of Australian birds) in *Amphibolurus* lizards (Bradshaw, 1971) or changes in the integument in mygalomorph spiders (Gray, 1968).

In widespread species, local populations may show adaptive responses of the type, but not the scope, shown by congeneric species occupying increasingly arid situations. One such case is the wide ranging parrot, *Barnardius zonarius*. This species is largest and most brightly coloured in the high rainfall area of southwestern Australia, but becomes smaller and duller towards the drier interior.

Hand-reared juveniles of the desert inhabiting populations were compared with similarly collected and reared juveniles of non-desert populations. Differences were demonstrated in metabolic rate, excretory water loss, food assimilation rate, amounts of water consumed and ventral feather reflectance. These factors were deemed to be genetically, not environmentally, determined. The physiological parameters exhibited a cline. Metabolic rate was lowest in Kalgoorlie birds and progressively higher at Tammin, Perth and Pemberton; other parameters followed a similar trend. Neither thyroid activity nor adrenal hormones were involved in the clinal or seasonal changes in metabolic activity (Nicholls, 1980).

This example suggests that selection for phenotypes capable of withstanding hot arid conditions is similar in principle to that for insecticide resistance or fluoroacetate tolerance.

The range of adaptive responses is likely to be greater among invertebrates than vertebrates. Their small size often permits behavioural avoidance of harmful conditions and different stages in the life cycle, with the possibility of diapause, may

lead to persistence in what might otherwise be intolerable environments. Unfortunately, the essential knowledge of the natural history and life cycles often is lacking.

Insects, like vertebrates, appear to have overcome the problems posed by toxic substances in their diet, for example in eucalypts which are eaten by a great variety of insects. Fox & Macauley (1977), investigated the ability of the larvae of the chrysomelid *Paropsis atomaria* to grow on the leaves of various *Eucalyptus* species with different levels of nitrogen, tannin and phenols. Northern Hemisphere studies have shown that tannins form indigestible complexes with proteins and so have the potential to reduce the nutritive value of plant food. In the studies of Fox & Macauley (1977), tannins did not appear to protect eucalypts from insect grazing. The high pH of the gut and rapid rate of passage were viewed as adaptations to the high tannin content of the leaves.

In dry or arid conditions, species of mygalomorph spiders in the genera *Anidiops*, *Aganippe* and *Idiosoma* have adapted to sparseness of food by attaching vegetation (twig-lines) to the rims of their burrows. This device permits the spider to become aware of potential prey at some distance from the burrow rim. Some populations are known from transitional habitats in which the offspring from a single brood show behavioural differences in the attachment of twig-lines. The basis of this is presumably genetic (B.Y. Main, 1957; unpubl.). Other adaptations by mygalomorph spiders to the hazards met with in arid environments are discussed by B.Y. Main (1982).

Darlington (1959) saw three sorts of adaptation: speciation, adaptations to special environments and general adaptations. He was interested in the development of dominant successful forms, that is, the ones which replaced the more primitive animals. He saw general adaptations as arising within the fauna of the large areas of the Old World Tropics and North Temperate Zones. Darlington's generalized adaptations were classifications based on history and perceived success, but the nature of the general adaptation was not detailed further. Brown (1958) saw special adaptations as fitting the organism or population to particular features of the immediate environment. General adaptations, in contrast, are concerned with internal organization and efficiency of the organism. Adaptation now is seen as more complex than as envisaged by these authors and classifications of general and special adaptations have not been pursued further. They have been addressed, however, within the framework of niche theory, life history strategies and physiological ecology. The results of these studies have yet to be synthesized in terms of general or special adaptation.

DIVERGENCE

Divergence proceeds in descendants of a single population split into two or more populations by the development of reproductive isolating mechanisms.

Indigenous fauna

The approaches possible in studying divergence fall into two groups.

(1) Those related to divergence *per se* such as:

- (a) the order or sequence in which forms diverged (cladistic analysis);
- (b) the origin and nature of the specific mate-recognition system which keeps diverged populations separate;
- (c) the degree of morphological or physiological difference resulting from divergence (adaptive responses);
- (d) the array of kinds resulting from the divergence (radiation);

(2) Those related to the possible causes of the observed divergence, especially what can be inferred from:

- (a) patterns of distribution;
- (b) possible barriers leading to fragmentation and speciation; and
- (c) contrasting causes of divergence such as ploidy, hybridisation.

The widely developed interpretation of divergence is that of allopatric speciation expounded by Mayr (1963). Paterson (1981) points out that allopatric speciation is the only theoretical model which has support from critical observations. The key observation in any hypothesis of allopatric speciation is that a pattern of clinal variation frequently is observed in wide-ranging species. The differences observed are often of the kind recognised taxonomically between species. Moreover, if a present continuous distribution was fragmented for a sufficiently long period, reproductive isolation would ensue and the speciation process would be complete. This is also consistent with the interpretations advanced by vicariance biogeographers. Sympatric occurrence is considered evidence of speciation in allopatry following a dispersal. How the divergent but effective social mate recognition or mating system arises in allopatry is important and needs study; especially significant is the role of small peripheral populations (West-Eberhard, 1983; Templeton, 1981; Carson & Templeton, 1984).

Another group of biologists is more impressed with patterns of sympatric occurrence. This group tends to discount interpretations based on allopatric occurrence preceding speciation. Instead it looks to mechanisms by which speciation could occur in sympatry; that is, that reproductive isolation be reached by a population derived from another while the two coexist. The question is what relative importance is to be ascribed to the two hypotheses and how mate recognition or a mating system arises in sympatry. The observational evidence for allopatric speciation is strong. That for sympatric speciation is theoretical, but empirical support is weak (Paterson, 1981; Futuyma & Mayer, 1980).

In Australia, some species of birds have ranges extending across the south while others have pairs of species, one species on each side of the central desert or the Nullarbor Plain. The latter pattern was interpreted as evidence of a former widespread species whose range was fragmented (Serventy & Whittle, 1951).

In the 1950's, the widely accepted model of the Pleistocene glaciations was that there were relatively few ice advances, each advance interpreted as heralding wetter conditions at lower latitudes. Conversely, ice retreat was thought to imply warmer drier conditions at low latitudes (Browne, 1945; Keble, 1947; Crocker, 1946). Crocker & Wood (1947) interpret disjunct distributions of plants as fragmentations of former widespread forms by the aridity related to the climatic changes associated with the post-Pleistocene retreat of the polar ice caps. These authors point out that some of these disjunct populations could be recognised as species, while others remained con-specific. Mackerras (1960) and Main *et al.* (1958) extend this hypothesis to account for examples of tabanid flies and frogs where a multiplicity of sympatric species occurred in the southwest of Western Australia while the closest relative occurred in the southeast of Australia. This hypothesis postulated that during periods of ice advance sea levels would be lowered and the cooler, wetter climatic conditions which then prevailed would permit a whole suite of cool, moist adapted fauna to disperse to the southwest. In essence, this was a hypothesis of speciation following a vicariance event. Dispersal occurred when there was no barrier, speciation occurred in an isolated peripheral population after the barrier was in place.

6. RADIATION OF TERRESTRIAL FAUNA

This model has been criticised by White (1978) and by other workers favouring other modes of speciation. The criticism has been especially directed at the interpretation for frog speciation in southern Australia. More recent hypotheses of low latitude climates associated with ice ages suggest that while the temperature may have been lower, precipitation also would be reduced. On the whole, the climate would be cooler and drier (Maxson & Roberts, 1984). These workers believe it would be too dry for frogs to disperse between east and west during the Pleistocene. More importantly, Barendse (1984) and Roberts & Maxson (1985) interpret allozyme data and immunological distances as indicating Tertiary separation of eastern and western frogs and speciation within southwestern Australia.

The observations which Main *et al.* (1958) attempted to explain can be interpreted as peripheral marginal populations (Mayr, 1963) of eastern species. In the case of the seasonally dry habitat of *Crinia*, the following argument was developed. The species pairs *C. parinsignifera* of the east and *subinsignifera* of the west were very similar in call. The next most similar call was *insignifera* and the least similar was *pseudinsignifera*. Comparison with other frog genera in southwestern Western Australia showed that there could be identified a similar grouping which could be taken as confirmation of the triple migration hypothesis. These migrations were postulated as being Pleistocene, which was reasonable in the light of the assumed relationships between ice ages and aridity and, in terms of the modern expression, was parsimonious because it did not require postulating undemonstrable barriers for allopatric species in Western Australia, an undemonstrable pattern of sympatric speciation or an age of speciation greater than the most recent known climatic fluctuations.

The late fossil record for southwestern Western Australia indicates that the marsupials *Phascalarctos* sp., *Vombatus* sp., *Sarcophilus harrisii* and *Thylacinus cynocephalus* were present in the late Quaternary (Merrilees, 1984).

These cases have been interpreted as dispersals from southeastern Australia into southwestern Australia during a wetter period when sea levels were lowered. In terms of vicariance theory, if there were connections between two localities the whole biota will likely disperse. Barendse (1984) suggests that patterns in these groups may be specious, may more reasonably be interpreted like the frogs and should be reinvestigated.

Palaeoclimatologists, with the benefit of a more comprehensive theory of ice age climates and a greater spread and depth of data, have been able to construct a more detailed picture of climate in the last Glacial. Bowler (1978; 1980; 1983; Chapter 1) postulates the two-phase nature of the last Glacial. The first phase in southern Australia was a cool, wet phase with full lakes and brimming rivers from 45,000 to 25,000 ybp. The second was an arid phase from 25,000 to 13,000 ybp dominated by a summer continental high pressure system. Under the influence of the hot strong winds generated during summer, vegetation was destroyed and longitudinal dunes became mobile. Bowler envisages the summer of this period as hot with intense drought, characterised by phases of strong hot dust-laden winds blowing from the centre of the continent. These episodes were terminated by cold fronts which moved across from the west, such as the frontal events which now terminate drought. Thus, the wheel has turned a full circle. An arid period, c.f. the Great Arid of earlier workers, again appears in interpretations, but is of greater age, its dimensions and causes better dated and related to a theoretical body of knowledge. The intensity of the dry phase of this last glacial has tended to obliterate traces of the earlier wet phase because lakes and swamps have had dune sands blown over them. Bowler, nevertheless, believes that similar wet/arid cycles were associated world-wide with

glacial advances back to 700,000 ybp. Such a prolonged series of oscillations between moderate climates and hot dusty droughts must have contributed greatly to the extinction of the fauna characteristic of earlier times. At the same time, selection would have been intense and range changes immense between drought and the subsequent climatic amelioration.

Interestingly, the physical deterioration of the climate documented by Bowler was accompanied by the extension of the range of *Macropus rufus*, (as shown by fossil occurrence) to what is now the outskirts of Melbourne (Horton, 1984). The climatic interpretation of this event is based on the present observation that *M. rufus* only occupies areas receiving an annual rainfall of less than 250 mm. He concludes that in the closing phases of the last glaciation, the arid core of the continent expanded immensely. This interpretation is consistent with the scenario of Bowler (1978; 1980) and is the sort of event postulated by Main *et al.* (1958) to account for the supposed extinction of the ancestral *Heleioporus* inhabiting seasonal swamps in eastern Australia.

All workers on the Antarctic agree that the continental ice of Antarctica is of greater age than that of the Arctic. Antarctica has been isolated climatically since the opening of Drake Passage and the subsidence of the Tasman Rise in the Oligocene. Snow cover was present in East Antarctica in the Eocene (Flohn, 1978), but the continental ice sheet only developed after the Oligocene. These cooling events, proceeding throughout the Tertiary, were the causes of the global ice ages and the drying of Australia. This event, with its numerous phases, has been the direct cause of the selective pressure leading to the divergence and, ultimately, the adaptive radiation of the Australian fauna.

The events of the Tertiary are not the only ones which have produced disjunct distributions in the fauna. In the Jurassic there were numerous lakes on the continent (Brown *et al.* 1968; Coleman, 1980) and during the Cretaceous the present continent was fragmented into a number of islands by epicontinental seas. This has been indicated by Laseron (1969), Brown *et al.* (1968) and Morgan (1980) and used by Key (1976) as a basis for the interpretation of some observed patterns in the eumastacid grasshoppers. Figure 6.1 shows the distribution of land during the Early and middle Cretaceous.

MacKerras (1960) interprets speciation in the fly genus *Scaptia* (Tabanidae) as relating to events ranging from Cretaceous to Pleistocene. Most of the dispersal had been from east to west, but there had been some reverse migration.

Possibly, the two sections of the mygalomorph spider genus *Aganippe*, whose distributions centre in Western Australia and central southern South Australia, as well as the genus *Blackistonia* centred there, may represent the derivatives of a fragmentation during the Cretaceous.

During the early Tertiary, the central Eyrian Australian lakes were large and Kluge (1967b) believes they were possibly the physical barrier that separated the ancestral Diplodactylini and Carphodactylini. Subsequently, the Diplodactylini evolved in relation to the eremean flora (Kluge, 1967b).

Within the lizards of the Australian deserts, Pianka (1972) recognises a number of groups and believes that in the habitat-specific genera, speciation has been due to habitat extension and fragmentation resulting from fluctuations in climate. These fluctuations particularly affected the extent of the sandplain-*Triodia* sand ridges and shrub-*Acacia* habitats and the possibility of dispersal along sand and shrub corridors is seen as particularly significant in the speciation process.

Cracraft (1982) interprets cladistic relationships among bird taxa and vicariance patterns among areas of endemism as evidence for allopatric speciation and proposes (his map, Fig. 6) a vicariance hypothesis for the Australian avifauna. The major postulated barriers separate the northern and eastern from the central and southern and lie between the central arid and southern mesic fauna. There are barriers postulated within each of these areas of endemism. A model such as that developed by Cracraft (1982) has the potential to include all the events from Cretaceous to Quaternary. Endler (1982), however, specifically rejects the prediction of vicariance biogeography that concordant cladograms should indicate common vicariance sequences. He believes that concordant cladograms can only result from common patterns of shared selection regimes and thus do not reflect vicariance patterns. He lays emphasis on distinguishing ecological from historical factors in species distributions.

Notwithstanding the answers obtained by cladistic analysis of morphological traits, prospective mates identify on shared derived characters such as social and courtship behaviour, male call, pheromones or other specific mechanisms for recognition. All the foregoing discussion has not advanced our understanding of how these specific recognition mechanisms arise other than to imply or assume that given long enough, they will arise in allopatry (but see Dominey, 1984; West-Eberhard, 1983).

The pattern of species distribution in the termite genus *Drepanotermes* questions the above assumption. This genus is derived from *Amitermes* and Watson & Perry (1981) show that the distribution centred about the northwest of Western Australia. By drawing arcs with radii at 500 km intervals, centred on North West Cape, they show a progressive decrease eastward. Within the first arc 19 species occurred. At successive intervals the number of species declined, so that with radii between 2,500 and 3,000 km only six species were found. Beyond 3,000 km only one occurred. Some species are widely distributed and these are highly variable. Watson (1982) suggests that speciation arose as a result of local divergence in response to special cues for the mating flights of alates. Should this be so, then it is in some ways analogous to the diversification discussed by Dominey (1984).

Putative mechanisms of speciation have been arranged by Templeton (1981) into a classification which recognises two categories: divergent (adaptive, clinal, habitat) and transilience (genetic from faunal event, chromosomal, hybrid maintenance or hybrid recombination). In addition he envisages the genetic basis of isolating barriers as three types: Type 1, many segregating units; Type 2, a few major segregating units; and Type 3, complementary or duplicate pairs of loci.

Carson & Templeton (1984) further develop models to account for the speciation seen in the picture-winged *Drosophila* of Hawaii. In these species, marked phenotypic differences occur with apparently only small changes in the genotype. The two aspects emphasised in the models favoured by Carson & Templeton (1984) are the founder flush and transilience. In the former, the founding population leads to a disruption of the coadapted gene complexes. Then follows a phase of disorganisation until the population establishes itself in a new environment. This is followed by a flush phase in which the population expands with little genetic variation being lost and recombination in the relaxed conditions is common. In transilience, the founder population derived with coadapted gene complexes has these changed through drift by changes in major loci, which results in drastic fitness reweighting of the pleiotropic effects associated with the major gene. Hence, strong selective forces are created shortly after the founding event determined by the



Figure 6.1 Outline of Australia with areas of land (stippled) and areas of sea (unshaded) for the Early and Middle Cretaceous. (After Morgan, 1980)

[H. Hunt]

altered genetic environment. For transilience to work, the founder population must have large genetic variability and numerous modified loci in order to respond.

Only when the restructured coadapted gene complexes and specific mate-recognition system are fully developed is the new species able to maintain its identity in sympatry. The models of Carson & Templeton (1984) and the studies of Watson & Perry (1981) imply that as evolutionists we should not lose sight of the fact that prospective mates identify each other on biological traits, whereas taxonomists identify species on character states which may not be cues for prospective mates.

Populations are frequently distinguished by differences in karyotype. Whether specific mate recognition systems are associated with karyotypic differences is unknown. Briscoe *et al.* (1982) review the chromosomal and allozyme differences in the rock wallaby genus *Petrogale*, in which the distribution of the differences suggests that they are in some way adaptively superior.

Mahoney & Robinson (1980) show that within the frog genus *Neobatrachus* two species (*N. sudelli* and *N. sutor*) are tetraploid. Whether they are autotetraploids or allotetraploids is not established. Should they be the former, it is difficult to see how the calls and genotypes could be restructured unless the populations were isolated. Should they be allotetraploids, they could have arisen when two formerly disjunct populations came into contact. Again, there is the problem of whether the genotype and male call could be restructured without being in a small isolated population. Despite these conceptual difficulties, there is no doubt that they are now successful species and *N. sutor* is very widespread.

Rates of Evolution

From the review of the possible physiographic conditions associated with the break up of Gondwana it is apparent that uncertainty exists about the last time that continuous land existed from Australia through Antarctica to South America. This has meant that rates of divergence cannot be readily calculated. The proposal that albumin proceeds in a rather clock-like fashion has been used by Maxson & Wilson (1975)

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in an attempt to date the divergence of Australian from South American hyline frogs. They validate the rate as a dating device for the Australian case the following way:

"the mean albumin immunological distance between Australian hylines (*Litoria*) and American hylines is approximately 129 units" ... "Assuming the normal rate of albumin evolution this corresponds to a divergence time of approximately, 75 million years. This is approximately the time when the last land bridge existed between Australia and South America via Antarctica (Cracraft, 1973). The disappearance of this land bridge may have been the event that separated Australian and American hyline frogs" (Maxson & Wilson, 1975).

Maxson *et al.* (1975) use recent studies on continental drift to test the albumin clock hypothesis by using data for marsupials and hyline frogs. The authors give the mean immunological distance from Australian species to *Didelphis* and *Metachirus* as 121 units whereas to *Caluromys* and *Marmosa* it is only 86 units. Because of this marked deceleration in the albumin change for *Caluromys* and *Marmosa*, they are ignored in dating the separation of the two marsupial groups.

The anti-*Litoria* immunological distances are higher than the reciprocated tests and the

"corresponding hyline distance is perhaps overestimated by giving the anti-*Litoria* values (mean 144) a weight equal to the nine New World anti-sera combined (mean 114). To check this anti-sera to additional Australian hyline frogs albumins are needed but till these are prepared it is probably best to accept 114 units as the best available estimates of inter continental distances" (Maxson *et al.*, 1975).

Maxson & Wilson (1975), however, use the mean of 129 units and not the value argued for above. Using a rate constant of 1.7 units per million years, Maxson *et al.* (1975) then calculate that if this holds for marsupials and hyline frogs one obtains a figure of 73 million years or 68 million years for the separation of the Australian and New World marsupials and hyline frogs, respectively, and go on to say

"these figures are consistent with current geological dating of the South American Antarctic separation occurring in late Cretaceous 70 million years ago" (Maxson *et al.*, 1975).

As their authority they cite Dalziel & Elliot (1971). These authors studied the deformation and intrusive events of the Andean orogeny and conclude that fragmentation could not have occurred before the end of the Mesozoic, but go on to conclude

"that sea floor spreading has occurred from at least mid-Cenozoic 20–25 million years ago until recent in Drake Passage. Hence the disruption and fragmentation of the Andean-West Antarctic Cordillera occurred in the early Cenozoic prior to 20–25 million years ago or else accompanied the spread of Drake Passage" (Dalziel & Elliot, 1971).

Maxson *et al.* (1975) acknowledge that the divergences may have occurred before the continents drifted or a more ancient divergence and slower rate of albumin evolution are consistent with their results, but argue against a younger separation of South America and Antarctica because eutherians would have got to Australia. Their final conclusion is as follows:

"We infer therefore that the lineages leading to living Australian marsupials and hylines diverged from those leading to their New World counterparts at a time that did not significantly predate the disappearance of the trans-Antarctic land bridge between these two regions" (Maxson *et al.*, 1975).

From the geological information reviewed earlier it is clear that the dating of the disappearance of the land bridge is no better now than when Dalziel & Elliot (1971) dealt with the matter. Avise & Aquadro (1982) and Avise (1983a) summarise the literature on electrophoretically assayed protein distances between species. Avise (1983b) discusses the variability among the clocks that might be employed in dating events and concludes that

"the major impediment to the possibility of a uniformly calibrated molecular clock is lack of critical fossil-based or biogeographic knowledge of avian (or any other vertebrate) speciation times" (Avise, 1983b; an opinion clearly supported by the marsupial and hyline examples cited above).

Apart from the difficulty of establishing fossil based rather than circumstantially determined dates for divergence, there are other aspects which cast doubt on the reliability of molecular clocks, namely, parallel evolution and different rates of fixation of mutants (Joysey, 1981) and the possible selective significance of protein and allozyme polymorphism (Nevo, 1983). Cain (1983) regards molecular clocks as myths.

RADIATION

Over long periods of time, adaptation and divergence naturally lead to many ecological and morphological differences. Such a result commonly is termed radiation. Radiation is, however, dependent on a combination of time, geographical and topographic diversity, ecological opportunity and a behavioural capacity to invade or take advantage of new expanding habitats. Thus, the oldest elements of the fauna need not necessarily have the most marked radiation. The monotremes, which are an extremely old element of the Australian fauna, have occupied only two habitats: one terrestrial (*Tachyglossus*, *Zaglossus*), the other aquatic (*Ornithorhynchus*). Some of this apparent simplicity may be due to extinctions. On the other hand, a most spectacular radiation is provided by the marsupials, though they do not occupy the same ranges of macroniches as eutherians (Lee & Cockburn, 1985). The range from insectivores, carnivores and herbivores of various kinds and sizes is, nevertheless, very impressive. The Australian passerines also have undergone a very marked radiation (Sibley & Ahlquist, 1985). A behavioural capacity to take advantage of the more open woodlands and grasslands which became common from Miocene times onwards was a likely prerequisite for radiation.

Examples of lesser radiations of the older elements are provided by the diplodactyline geckos, the pygopodids and the hylid frogs. The genera *Litoria* and *Cyclorana* have radiated in behaviour and morphology so that frogs ranging from aquatic, terrestrial, arboreal and burrowing desert forms are to be found.

Among the invertebrates, the morabine grasshoppers appear to have had some of their radiation at the tribal level initiated on the islands formed by the shields of Australia during the period of high Cretaceous seas (Key, 1976). Diversity within this tribal radiation appears to be related to areas of high relief (Key, 1976).

Howden (1981) gives further examples from the Scarabaeoidea of taxonomic diversity in some of the older (Mesozoic) elements of this part of the fauna. Interestingly, the elements occupying the central deserts are attributable to the older faunal elements.

Among the termites there has been a pronounced exploitation of the harvesting niche. The genus *Amitermes* (Amitermitinae) has several species which harvest grass or plant debris. From it has been derived the widespread *Drepanotermes*, whose speciation pattern has been mentioned

above. *Nasutitermes triodiae* (Nasutitermitinae) harvests grass and the large endemic genus *Tumulitermes* is common in the drier inland parts of Australia where it harvests grass and other plant debris.

The aganippine trapdoor spiders are a southern group which appear to have their first division between those on the Western Shield and those of the Flinders Ranges. In each of these groups there has been a parallel radiation so that species now occupy habitats ranging from damp stream banks through sclerophyllous woodland to mallee, mulga and dune fields. Associated with each of these habitats is an accompanying suite of morphological, physiological and behavioural traits (B.Y. Main, 1982).

As more is learnt about the biology and taxonomic diversity of other components of the old fauna, more extensive radiations undoubtedly will become apparent. In this regard, the blattids of the subfamily Polyzosterinae offer great potential. The newer fauna has had less time to radiate, but the rodents show that even a Tertiary arrival still had time for the occupation of a variety of habitats (Baverstock, 1984). The example of the rodents is of interest because the diversity within the group is such that, as mentioned earlier, it is considered the result of multiple invasions of Australia by different stocks.

There are undoubtedly other groups in the fauna where, as in the case of the rodents and passerine birds, once the phylogenetic relationships can be established, the extent of radiations that have occurred may be perceived.

In contrast, a number of widespread species or genera are either monotypic or have very few species, only one of which is widespread. Examples are: the monotreme *Tachyglossus aculeatus*, the pygopodid *Lialis burtonis*, the scincid *Trachydosaurus rugosus*, the agamid *Moloch horridus*, the gekkonids *Heteronotia binoei* and *Rhynchoedura ornata* and the mygalomorph spiders *Aname diversicolor* and *Chenistonia tepperi*. Such examples give no indication of incipient divergence which might be taken as the beginning of a radiation. The cause may be inadequate taxonomy. Until the revision of Watson & Perry (1981), the termite *Drepanotermes rubriceps* would have been similarly regarded. Moreover, King (1983; and earlier papers) has shown that within what were formerly regarded as wide ranging species of gecko, there may be distinct karyotypes.

These widespread forms are difficult to interpret because they can be regarded as old elements of the fauna, unlike for example, the skink *Cryptoblepharus boutonii*, which in its several forms, is widespread and might be interpreted as a relatively recent migrant. There seem to be several possible explanations: a characteristic of the wide ranging spiders is that they are not habitat specific but occupy a wide range of vegetation types. This suggests that they either have a wide physiological tolerance, are long lived or have a good behavioural repertoire for avoiding the deleterious effects of the environments in which they live. The lack of habitat specificity and broad tolerances (a large fundamental niche) would tend to reduce the chances of population fragmentation (see Pianka, 1972) and so vicariance barriers may never have operated. On the other hand, the widespread occurrence at present may represent a range expansion from a refuge occupied during a relatively recent climatic deterioration in which other related species become extinct. Thus, the present wide range would represent the result of ecological release. The significance of extinctions cannot be readily assessed. The lack of habitat specificity, however, appears to be an important factor contributing to their wide distribution. Conversely, habitat specificity might be the prime factor initiating divergence and ultimately radiation.

When Lee & Cockburn (1985) discussed the radiation of marsupials, they were concerned with the extant forms. When the extinct forms are included, however, the radiation is much more impressive. Clearly, our perception of the extent of a radiation is contingent upon what we can know of the present biology or of the fossil record. In particular, we should be conscious that extinctions in the recent past may have left apparent gaps in the present structure of ecosystems.

EXTINCTIONS

Information on extinctions can be gathered from three sources: (a) from historical records. These are related to the conspicuous readily collected animals such as mammals and birds. These animals were collected and recorded by early collectors but now no longer occur in the place where first collected or are no longer known; (b) from patterns of distribution which are frequently disjunct or highly fragmented. Such ranges were formerly continuous and the present day breaks clearly relate to extinctions in the unoccupied areas; (c) fossils. These are or may be of extant animals which are: not at the fossil site, related but distinct from present day survivors or have no present day relatives.

Extinctions under (a) above are mostly related to habitat destruction or the effects of introduced animals.

Many of the past extinctions indicated by present disjunct distributions occurred long ago and most are unlikely to have been induced or influenced by Aboriginal man. The most likely cause of fragmentation is climatic or environmental change. As the biota becomes better known, this type of extinction leading to fragmented ranges is being documented in plants, invertebrates and vertebrates.

The fossils most readily studied are those of vertebrates and the pollen of plants. Fossils of terrestrial invertebrates are less studied because they are less readily fossilised and inherently more difficult to identify because the invertebrate fauna is much less known than the vertebrates. Moreover, vertebrate fossils have excited interest because they often represent bizarre distinctive animals which are much larger than present day animals and have no living descendants. Reviews of the animals which became extinct and the possible causes have been given by Murray (1984), Horton (1984) and Merilees (1984). Characteristic of these radiations recorded by fossils are the many large or very large animals. Broadly, the increase in size shown by the fossil record is in step with the decline in the environment, particularly increase in aridity of the continent.

Large size of mammals is a phenomenon of world wide occurrence during the Tertiary when climatic changes similar to those outlined by Bowler (1978; 1980) for Australia were widespread. The evolution of large size presumably relates to some selective advantage. The most significant relationship of size is to metabolic needs such as nutrition, which increases with increase in size or weight to $3/4$ power. This means that while larger animals require greater quantities of food, that is bulk, their requirements expressed in terms of unit of body mass decline. The increase in body size implies that large animals were evolving to take advantage of an increasingly bulky but less nutritious diet. The corollary is that smaller animals could be more selective in choosing quality dietary items and where to live.

Hofmann (1973) classifies African ungulates according to diet into concentrate (high quality diet), mixed and bulk and roughage feeders. These are not exclusively related to size. Main (1986) categorises macropods and compares them with African ungulates. *Macropus robustus* and *M. fuliginosus* appear to be bulk and roughage feeders. In terms

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of the surviving marsupials, there are two classes with respect to the digestive nutrition: (a) the macropodids in which varying degrees of ruminant-like digestive function can take place. With poor quality diet these delay the rate of passage of the ingesta and, if there is fermentable carbohydrate in the diet, may successfully recycle urea; and (b) the wombats which depend on caecal fermentation. With poor diet, such animals increase their rate of passage so that more ingesta is made accessible for extraction of nutrients. While the digestive systems of extinct forms are unknown, it seems likely that macropodids were ruminant-like in their nutrition while the large vombatids and diprotodontoids may have had a system dependent on caecal digestion. From Murray (1984) and the above, herbivores of both types seemed to increase in size as the abundant food decreased in quality. Grass would be common after summer rain or as very frequent fire destroyed shrub regeneration. Grazers would be favoured. Whatever their digestive processes, browsers would be dependent on the periodic regeneration of shrubs and browse, as at present, after infrequent fires. Concentrate, mixed, and bulk and roughage feeders would be found among both grazers and browsers.

Main & Bakker (1981) and Horton (1984) believe shortage of water contributed to the extinction of the large marsupials. Large slow-breeding animals were at a disadvantage because of their inability to quickly repopulate large areas from refugia once climate ameliorated (Main, 1978). Horton (1984) has documented the range extension of *Macropus rufus* during the last extension of the arid core of the Australian desert. This extension is coincident with the aridity documented by Bowler (1980). Horton uses these events to interpret the extinction of the large Australian marsupial fauna as being due to climatic deterioration and not hunting by Aborigines. Interestingly, the surviving herbivorous marsupials are mostly macropodids. These, ruminant-like in their nutrition, have an advantage over non-ruminant animals at times of decline in dietary quality. Their ability to recycle urea permits a slower rate of weight loss and a longer period before starvation leads to death; they can accommodate a seasonal shortage of food (see also Janis, 1984). This function, along with decline in size (Main, 1978), may have contributed to their survival to the present. Thus, extinctions are associated intimately with our concepts of extant radiations. To the extent that we are unable to unravel the biology of the extinct forms we will be unable to appreciate fully the extent to which marsupials, for example, radiated and exploited the available environments.

CONCLUSION

In the Introduction, questions were posed about the possible causes of the unbalanced nature and lack of taxonomic diversity in the fauna. The evidence reviewed does not lead to any definitive answers.

The fragmented nature of the land mass during the Cretaceous could have been the initial cause of low diversity in the pririfting regional Gondwanan fauna. The geological evidence reviewed gives no basis for determining the last time, in pririft Gondwana, that overland dispersal was possible. The presence of marsupials, ratite birds, frogs and a considerable variety of invertebrates suggest that an Australian-South American faunal interchange was possible. Whether it was over land, a filter bridge, an archipelago or dispersal over a water gap is not clear. The differences between Australian and South American passerines and absence of palaeoendemic eutherians in Australia needs explanation.

Faunal relationships with Asia suggest repeated invasions from that continent from the middle Tertiary. The adaptations of the introduced and indigenous fauna suggest that the basis of the adaptive phenotypic response is genetic. In the introduced fauna, phenotypic responses have arisen and been selected over a very short period. In the indigenous fauna, many adaptive responses were generated by the Miocene and post-Oligocene environmental changes and subsequent Pliocene-Pleistocene climatic deterioration. The climatic changes of this last period contributed to faunal extinctions as well as being the selective agent for the origin of extant drought and heat tolerant types.

From Mesozoic times, there have been repeated opportunities for splitting and divergence of populations. Possible agents have been epicontinental seas, lacustrine conditions, extensive tussock grassland separating woodlands, dune fields and climatic fluctuations leading to the extension and contraction of the central arid core. All these events could have fragmented extensive populations and formed peripheral isolates, some of which may have been adaptively superior under the changing conditions. Coupled with social and mate recognition systems such changes have led to divergence and radiations.

An extensive radiation of autochthonous elements occurred while Australia was isolated in its northward drift prior to suturing with Asia. These radiations are the characteristic Australian fauna. Nevertheless, some of the Asian elements have radiated since their arrival.

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7. THE INLAND AQUATIC ENVIRONMENT AND ITS FAUNA

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INTRODUCTION

There are many similarities between the fauna of Australian inland waters and the aquatic fauna of other continents. All major groups of aquatic animals are represented in Australia. The general faunal composition of specific habitats (such as highland streams, freshwater lakes, temporary rainpools) is the same in Australia as elsewhere. On the other hand, long geographical isolation, a generally flat topography and an overall climatic aridity have imposed conditions in Australia which have led to the development of a fauna with many special adaptations and which is both depauperate and diverse, different and similar to that on other continents. A fauna has developed which is distinctively Australian.

This Chapter briefly describes the major features of the inland aquatic environment, then considers the composition and distribution of the aquatic fauna. The latter consideration, it should be noted, gives unequal treatment to individual groups of animals, a fact which reflects our perceptions of the overall importance of groups and the extent of available knowledge. Finally, the Chapter summarizes the important distinctive features of the fauna. The evolution and adaptations of the fauna are considered in Chapter 8.

MAJOR FEATURES OF AUSTRALIAN INLAND WATERS

To appreciate fully the nature of the fauna of Australian inland waters, an awareness of the principal features of the Australian inland aquatic environment is needed. This Section outlines these features.

The General Distribution of Inland Aquatic Habitats

The extent of surface water on any continent is determined by the balance between precipitation, evaporation (or evapotranspiration) and runoff. Only Greenland and Antarctica have lower precipitation than Australia. Australia has a lower runoff than any continent (Fig. 7.1). As a consequence, aquatic habitats are relatively scarce.

Precipitation and evaporation vary seasonally and, therefore, so does the extent of aquatic habitat. In southeastern and southwestern Australia, rainfall either is comparatively even throughout the year or is greater in winter (June-August). Since evaporation is also lowest in winter, runoff also peaks in winter and fills wetlands, lakes and streams. Both permanent and temporary water-bodies are abundant in this region, but non-permanent bodies of water tend to be seasonal, regularly drying in summer and filling in winter and spring.

In central Australia, annual rainfall is extremely low, with a median value <200 mm per year, while mean annual evaporation exceeds 3,200 mm. As a result, there is virtually no surface water, except after occasional and irregular rainfall events which are most common in summer. Most aquatic habitats, therefore, are temporary and episodic. The exceptions are: specialized habitats such as mound springs fed by artesian water, a few permanent pools in episodic rivers and man-made bodies of water such as stock watering tanks.

In northern Australia, rainfall is monsoonal with a peak in summer and almost no rain in winter. Evaporation usually peaks in November since it depends on solar insulation which is reduced by cloud cover during the summer "wet". As a result, runoff is highly seasonal with a summer peak. Temporary habitats are also seasonal, filling in summer.

A brief inspection of a map of median annual runoff for Australia (Fig. 7.2) indicates the areas where aquatic habitat is most abundant. For most of the continent, the annual runoff is <10 mm for five years in every ten. The areas with significant runoff include a strip across northern Australia, including the Kimberleys, Arnhem Land and Cape York Peninsula, all of which are monsoonal with a highly seasonal rainfall, and a narrow strip down the eastern coast. There is also a small area in the southwest of Western Australia.

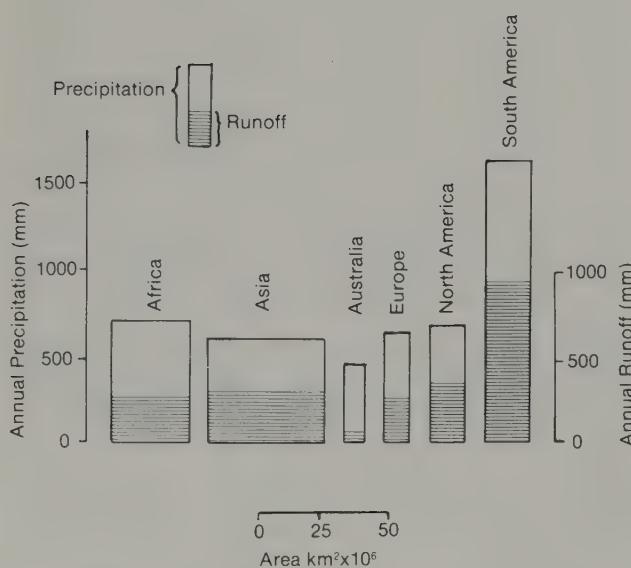


Figure 7.1 Precipitation and runoff for the major continents. (After Brown, 1983)
[R. Evans]

The Nature of Standing Waters

Except in Tasmania, large freshwater lakes are uncommon in Australia. On the mainland, the predominant natural standing waters are billabongs (a term applied both to ox-bow lakes and permanent pools associated with temporary streams), saline lakes, especially in the large endorheic and arheic drainage areas (Fig. 7.3), and wetlands. Man-made farm dams and ponds are also extremely common and reservoirs are numerous. Tasmania has numerous of lakes formed by Pleistocene glacial activity (Williams, 1974), but there are only six small lakes of this type on the mainland, all near Mt Kosciusko. A variety of other mechanisms has been responsible for the formation of lakes in Australia. Dune lakes are quite common in several areas on the east coast, notably on Fraser Island and nearby coastal areas in Queensland, and numerous lakes are the result of volcanic activity, especially in western Victoria. The largest lakes, such as Lake Eyre, are of tectonic origin.

The distinctive chemical features of Australian standing waters have been reviewed a number of times by Williams and co-workers (Williams & Wan, 1972; Bayly & Williams, 1973; Williams, 1980b). Buckney (1980) recently confirmed the earlier statements that sodium and chloride are usually the dominant ions in standing waters in this country. The general pattern of dominance in Australian saline lakes is: $\text{Na} > \text{Mg} > \text{Ca} > \text{K} :: \text{Cl} > \text{SO}_4 > \text{HCO}_3 + \text{CO}_3$. A similar pattern occurs in freshwater lakes, but with the relative importance of Mg and Ca and $\text{HCO}_3 + \text{CO}_3$ and SO_4 sometimes reversed. In contrast, Ca and HCO_3 are dominant in world average fresh water (Bayly & Williams, 1973). Most of the saline lakes and many of the natural freshwater lakes in Australia are shallow and, at least partly as a consequence of this, are also relatively turbid.

The pattern of thermal stratification is also distinctive in Australian lakes. The common Northern Hemisphere dimictic pattern, in which a lake is stratified in summer and winter with periods of mixing in spring and autumn, rarely is recorded in Australia. Most commonly, Australian lakes are warm monomictic, stratifying in summer and mixing in winter. Less common, but certainly not rare, are polymictic lakes which never stratify for long periods (Williams, 1983a).

Lakes, particularly shallow ones, may be quite variable in time both physically and chemically. Water temperatures vary seasonally with air temperatures, peaking in summer. Conductivity is least in wet periods and greatest in dry. There may also be variability in pH, particularly during periods of high primary production (Buckney, 1980). Saline lakes tend to have much more variable salinities (or concentrations of total dissolved solids) than do freshwater lakes. Bayly & Williams (1973) record a change in total dissolved solids for one small saline lake from 339 g L^{-1} to 17.2 g L^{-1} within a six month period.

The Nature of Flowing Waters

Lake *et al.* (1985) identify several distinctive features of Australian streams. High coefficients of variation of discharge are characteristic of arid zone streams, so it is not surprising that discharge in Australian streams overall should be variable. Variability of discharge, however, is greater for Australian arid zone streams than for those from arid areas elsewhere. More significantly, the discharge of streams in higher rainfall areas of Australia is far more variable than for streams in similar rainfall areas elsewhere (McMahon, 1982).

The biological communities in streams often derive a substantial proportion of their energy from leaves and other plant material which fall into the stream (Petersen & Cummins, 1974). The riparian vegetation of Australian streams is pre-



Figure 7.2 Median annual runoff values (in mm) for Australia.
(After Brown, 1983)



Figure 7.3 Major drainage regions for Australia showing the arheic region, the endorheic Lake Eyre drainage, the Murray-Darling, an exorheic basin and the coastal exorheic drainages.
[R. Evans]

dominantly evergreen with maximal leaf fall in summer (Lake *et al.*, 1985). Thus, most of the leaf input to the stream occurs when water temperatures are highest and, in southern Australia, when discharge is lowest. In contrast, Northern Hemisphere streams, such as those of Europe and North America, flow through either deciduous or conifer forests. In both cases, leaf or needle inputs are maximum in autumn (Triska *et al.*, 1982) when stream temperatures are lower and discharges higher. In addition, bark forms a higher proportion of the allochthonous organic inputs into streams in Australia than elsewhere due to the high proportion of riparian eucalypt species which decorticate. Bark is quite refractory in streams and, as a result, is probably not a

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Table 7.1 Present status of taxonomic knowledge of aquatic fauna of Australia. *+, little taxonomic information available; ++, not well worked taxonomically; (+)++, in part well worked taxonomically, in part not well worked.

FAUNAL GROUP	STATUS OF TAXONOMIC KNOWLEDGE*
Protozoa	+
Porifera	+++
Cnidaria	+
Platyhelminthes (Turbellaria, Temnocephaloidea)	++
Nemertea, Nematoda, Nematomorpha, Gastrotricha, Tardigrada	+
Rotifera	(++)++
Polychaeta	++
Mollusca (Gastropoda, Bivalvia)	++
Annelida (Polychaeta, Oligochaeta, Hirudinea)	++
Hydracarina	++
Crustacea:	
Anostraca	+++
Notostraca	+++
Conchostraca	+
Cladocera	++
Ostracoda	(++)++
Copepoda	(++)++
Branchiura	+
Syncarida	++
Isopoda	++
Amphipoda	++
Decapoda	(++)++
Insecta:	
Collembola	++
Plecoptera	+++
Ephemeroptera	++
Odonata	(++)++
Hemiptera	(++)++
Megaloptera	+++
Neuroptera, Mecoptera	++
Diptera	(++)++
Hymenoptera, Lepidoptera	+
Trichoptera	(++)++
Coleoptera	++
Pisces	(++)++
Amphibia	(++)++
Reptilia	(++)++
Aves	+++
Mammalia	+++

significant source of energy for the stream community. It does seem to provide, however, a significant habitat for invertebrates.

The suggestion that Australian streams may be less diverse than those elsewhere (e.g. Williams & Wan, 1972; Winterbourn, 1980) has been disputed by Lake *et al.* (1985). They show that streams in southeastern Australia are at least as diverse as those elsewhere. A comparison of species richness on stones between an Australian temperate stream and streams in tropical and temperate American streams (Doeg & Lake, 1981) indicates that the Australian stream is more similar to the tropical stream than to the temperate stream.

A number of studies on the life histories of Australian stream insects has found that they are flexible and poorly synchronized (Hynes & Hynes, 1980; Campbell, 1986; Marchant *et al.*, 1984). This has not been true, however, for all insects investigated. The number of published studies is small and it is difficult to determine to what extent lack of synchrony is a general characteristic of the Australian fauna. Most of the Australian species found to have synchronous life histories were studied at high altitudes or cool sites and it may be that

reduced life history synchrony is simply a response to higher water temperatures. Most Northern Hemisphere studies have been conducted at higher latitudes than the Australian studies (Lake *et al.*, 1985). Clifford *et al.* (1973) previously have suggested that life history synchrony of mayflies decreases toward the equator.

Although temporary streams are clearly of great importance in Australia and are the only streams present over much of the country, there is almost no information available on their ecology (Boulton & Suter, 1986). Most of the work which has been carried out either is concerned primarily with the ecology of single species (e.g. Marchant, 1982; Smith & Pearson, 1985) or remains unpublished. The only published comprehensive study is that of Towns (1983; 1985) on a small temporary headwater stream near Adelaide. He found an unusual fauna with a variety of adaptations to their temporary habitat, but this is too limited a data set from which to draw general conclusions about the nature of temporary stream communities in Australia.

Other Habitats

There are varieties of other inland aquatic habitats in Australia which are less numerous than those discussed above but of no less interest. These include mound springs, limestone springs and underground waters. Being less common, they have attracted less scientific study and public attention. They are also more prone to destruction. Mound springs, which are natural impoundments of released artesian water found overlying the Great Artesian Basin, are subject to damage from stock trampling and, perhaps even more significantly, overexploitation of the groundwater resource which leads to a lowering of the water table. Concern also has been expressed about the potential impact of diving and other human activities on the limestone springs in the southeast of South Australia. There are extensive areas of underground water in parts of Australia, but little is known about the biota of such systems (Williams, 1981a). Certainly, water which occurs in underground caves often contains a distinctive fauna.

COMPOSITION AND DISTRIBUTION OF THE FAUNA

A thorough knowledge of the composition of the fauna of Australian inland waters, especially its invertebrate component, lies in the future. Nevertheless, due mainly to work of recent decades, a reasonable amount of taxonomic knowledge is available for most vertebrate groups as well as several important and interesting invertebrate groups. Our knowledge of what animals are present in Australian inland waters has passed the exploratory stage and is sufficient to provide a firm and respectable basis for most general ecological investigations. Lack of taxonomic knowledge is a constraint for some particular ecological investigations and a significant impediment to the use of biological monitoring as a tool to measure water quality. Though incomplete by, for example, European standards, our knowledge of the Australian aquatic fauna is more advanced than that of the inland waters of South America and most of Asia and Africa. Table 7.1, an update and extension of tables previously published by Campbell (1981a) and Williams (1983a), indicates the present status of taxonomic knowledge of the aquatic fauna of Australia.

The general composition of the aquatic fauna of Australia is not grossly different from that of inland waters elsewhere, standing or flowing, fresh or saline. For example, copepods, cladocerans and rotifers dominate lake plankton, insects are important in fast streams and notostracans, anostracans and

conchostracans characterize many temporary water-bodies. At the same time, there are so many particular differences, involving both endemicity at several taxonomic levels and, in some cases at least, profound changes in the balance of faunal groups present in a given ecosystem, that almost all animal groups present in Australian inland waters possess a distinctive regional complexion. The only exceptions appear to be provided by the Protozoa, Nematoda and Polyzoa.

The following discussion will consider the nature of this regional distinctiveness on a systematic basis. It will outline briefly the composition of a particular group and consider its distribution (both ecological and geographical). An indication of research needs also will be given and brief reference made to important sources of information. A comprehensive general source of information on all invertebrate groups is provided by Williams (1980a).

Lower Invertebrate Phyla

Taxa informally regarded here as the lower invertebrate phyla are the Protozoa (or its several component phyla), the Porifera and the Cnidaria. Of these, the Protozoa is exceptional for, as indicated, it does not display any obvious regional distinctiveness. Most genera of Protozoa recorded from Australian inland waters are of cosmopolitan distribution. Little further attention need be given them other than to note that already over 50 genera of Mastigophora and 30 in each of the Rhizopoda and Ciliata have been recorded. All water-bodies, from highly saline lakes to ephemeral pools, contain protozoans, though detailed investigations of them in most types of habitat in Australia have still to be undertaken. Those genera of Protozoa most frequently recorded from Australian waters are listed in Table 7.2. One genus, *Euploites*, is illustrated in Fig. 7.4a.

A much greater degree of regional distinctiveness is shown by the freshwater sponges (Spongillidae). Approximately half of the 24 species known are endemic and the genus *Heterorotula* probably arose in Australia. *Spongilla alba* and *Ephydatia fluviatilis* may be recent introductions. The production of small and resistant gemmules has led to wide distributions for at least some species, but sponge distributions are by no means uniform throughout the continent. Freshwater sponges have been recorded from all States. For the most part, fresh or only slightly saline waters are favoured. A sound basis for taxonomic knowledge of the Porifera in Australian waters has been provided by Racek (1969), but next to nothing is known about their ecology in Australia.

Though most members of the Phylum Cnidaria are marine, a few occur in inland waters and in Australia four families accommodate such forms. The Hydridae (hydras), an entirely freshwater family, is represented by at least two cosmopolitan forms, *Hydra oligactis* and *Chlorohydra* (possibly *C. viridissima*), and one endemic form, *H. hexactinella*. The Clavidae, a mostly marine family, is represented by *Cordylophora*, a sessile, colonial, hydroid-like form. The Olindiidae is represented by *Craspedacusta sowerbyi* (Fig. 7.4b), of which the most obvious life-stage is a small, free-floating jellyfish. The Australomedusidae, an endemic family, is represented by *Australomedusa baylii*, known only from its medusoid stage. Hydras are known from many ponds, streams and freshwater lakes in Australia, but have not been subject to any detailed investigation. *Cordylophora* (probably *C. caspia*) also occurs in standing and flowing waters. It has been found in both fresh and moderately saline waters in Victoria. *Cordylophora sowerbyi* occurs widely throughout the continent, albeit sporadically. *Australomedusa baylii* is found in saline lakes near the coast which lack direct marine

Table 7.2 Protozoan genera most frequently recorded for Australian inland waters. (After Williams, 1980a)

MASTIGOPHORA	RHIZOPODA	CILIATA
<i>Salpingoeca</i>	<i>Amoeba</i>	<i>Podophrya</i>
<i>Chromulina</i>	<i>Arcella</i>	<i>Lagenophrys</i>
<i>Mallomonas</i>	<i>Diffugia</i>	<i>Paramecium</i>
<i>Dinobryon</i>	<i>Cryptodiffugia</i>	<i>Coleps</i>
<i>Cryptomonas</i>	<i>Euglypha</i>	<i>Loxophyllum</i>
<i>Euglena</i>	<i>Sphenoderia</i>	<i>Spirostomum</i>
<i>Phacus</i>	<i>Trinema</i>	<i>Stentor</i>
<i>Lepocinclis</i>	<i>Actinosphaerium</i>	<i>Vorticella</i>
<i>Trachelomonas</i>	<i>Actinophrys</i>	<i>Carchesium</i>
<i>Menoidium</i>	<i>Clathrulina</i>	<i>Epistylis</i>
<i>Volvox</i>		<i>Stylonichia</i>
<i>Chlamydomonas</i>		<i>Euploites</i>

connection. Apart from distributional records, little is known about either *Cordylophora* in Australia or the Australomedusidae.

Pseudocoelomate and Acoelomate Phyla

Several phyla, more "advanced" than those just discussed, can be grouped conveniently by their common lack of a coelom, that is, their lack of the type of body cavity developed within embryonic mesoderm and found in all "higher" invertebrates (notably, molluscs, annelids and arthropods). These pseudocoelomate and acoelomate phyla are the Platyhelminthes, Nemertea (or Rhynchocoela) and Aschelminthes (Phyla Nematoda, Nematomorpha, Rotifera and Gastrotricha). The groups involved are of quite unequal importance within inland waters; only the Platyhelminthes, Nematoda and Rotifera are common and widespread.

Of the six commonly recognized platyhelminth classes, the Turbellaria and the Temnocephaloidea are of direct interest in the present context in that they have free-living adult aquatic stages. The occurrence of free-swimming larvae of some trematodes, however, should be recorded.

In the Turbellaria, as well as the large and familiar triclad (flatworms), all orders of the microturbellaria are known from Australian inland waters (Sluys, 1986; Table 7.3). Rather little is known about the microturbellaria, partly reflecting the relative difficulty of preserving specimens for examination. It is known, however, that most are free-living, but that *Didymorchis* lives ectocommensally in the branchial chambers of the crayfish genera *Cherax* and *Euastacus*. Triclads, too, need special preservation for proper study, but recent work is providing a firm basis for their taxonomy (Ball, 1974; Hay & Ball, 1979). Eight genera have been described, most within the Dugesiidae. This family also is found outside Australia, but reaches its greatest diversity on the Australian continent. Many triclad genera are endemic. *Eviella* and *Reynoldsonia* are confined to Victoria, *Neppia* and *Romanenkia* to Tasmania. *Spathula* also occurs in New Zealand. *Cura* and *Dugesia* (Fig. 7.4d) are found outside Australasia. All of these genera have free-living species. Another genus, *Bdellasiomilis*, with the single species *B. barwicki*, is a leech-like turbellarian which inhabits the limb-pits of certain species of freshwater turtle in eastern Australia. Turbellarians generally are found in fresh waters, but at least one species (*Mesostoma*) has been recorded from salt lakes.

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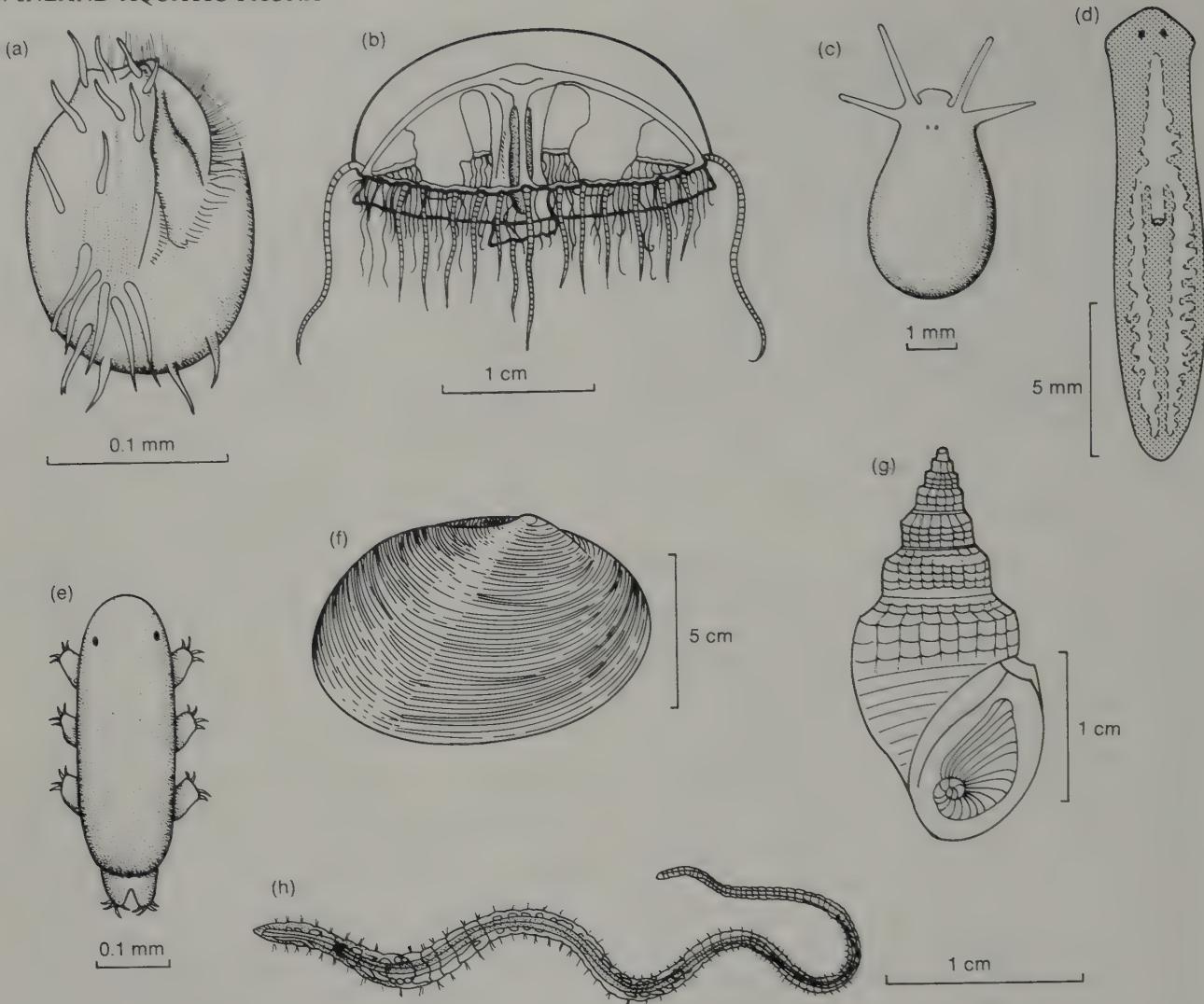


Figure 7.4 Some invertebrates of Australian inland waters other than arthropods. (a) *Euplates* (Protozoa); (b) *Craspedacusta sowerbyi* (Cnidaria); (c) *Temnocephala quadricornis* (Temnocephaloidea); (d) *Dugesia* (Turbellaria); (e) *Macrobiotus* (Tardigrada); (f) *Velesunio* (Bivalvia); (g) *Plotiopsis* (Gastropoda); (h) *Tubifex* (Oligochaeta). (After Williams, 1983a)

[R. Evans]

Unlike most turbellarians, the temnocephalids (Fig. 7.4c) are all ectocommensals and their main hosts are various freshwater crustaceans (crayfish, phreatoicoids, atyid and palaemonid prawns, potamondid crabs). They occur either in the branchial chamber or on the outer body surface of hosts. Although temnocephalids are found outside Australia (India, southeastern Europe, Central America), the group as a whole is most abundant and diverse in Australia. Fifteen Australian species have been described to date and several undescribed forms are known. Temnocephalids are recorded from all States except the Northern Territory. A most interesting group, it is surprising that a study of their taxonomy and biology is so long overdue.

Nearly all nemerteans are marine. A few occur in fresh waters and, of these, *Prostoma* is the most common. Rare animals frequently overlooked by biologists, nemerteans are more or less confined to small, permanent, weedy ponds and backwaters of rivers and streams. The only species recorded in Australia is *P. graecense*, though even it may have been introduced. It is widespread beyond Australia.

In marked contrast to the Nemertea, nematodes are ubiquitous and amongst the most abundant animal groups found in inland waters. Here, they occur in most types of water-body, sometimes the same species in different types. Despite

their abundance and widespread distribution, little work has been concerned with the nematodes of Australian inland waters and relatively little even with those of inland waters worldwide. On present indications (Nicholas, 1975), probably most Australian genera and many species will prove to be cosmopolitan or widespread. The three main families with free-living freshwater representatives are the Dorylaimidae, Plectidae and Trilobidae.

The Nematomorpha, although allied to the Nematoda, does not approach its importance and abundance. Adults are found free-living in fresh waters, but arise from a larval form which parasitizes aquatic or (mostly) terrestrial insects. Some Australian species have been described and six genera, none endemic, have been recorded in Australia (*Gordius*, *Acutigordius*, *Gordionus*, *Parachordodes*, *Pseudochordodes* and *Chordodes*). All present records are from eastern Australian localities, but it is, of course, most unlikely that nematomorphs are absent from the western half of the continent. No modern, comprehensive treatment exists which deals with the regional characteristics of the group.

The Rotifera is about as widespread in inland waters as the nematodes. Generally freshwater forms, a few species are known from saline lakes. The extremely small size of most species and the consequent likelihood of wide dispersal were

taken previously to indicate that most rotifer species were cosmopolitan or widespread. Recent investigations (e.g. Shiel & Koste, 1986), have shown that Australian species have a much greater degree of endemism than was originally thought. Of the 600 species so far recorded from Australia, about 15% are endemic. This fraction is expected to increase with further knowledge. The number of known species is regarded as probably only half the actual total. Over half of the recorded species seem to have restricted geographical distributions. Several distributions are disjunct or anomalous, though forms in the north clearly have affinities with the Indo-Asian fauna.

Like the Rotifera, the Gastrotricha comprises small acelomates (usually <0.5 mm long). For the most part they are confined to standing bodies of fresh water. Gastrotrichs have been poorly studied worldwide. The suggestion has been made that whilst most genera may be cosmopolitan, many species have more restricted distributions. This remains to be proved for Australian inland waters. Only a single genus, *Chaetonotus*, has been recorded from Australia.

Coelomate Phyla other than the Arthropods and Vertebrates

There are four non-arthropod, invertebrate phyla which possess a coelom found in inland waters. Two are relatively unimportant (Polyzoa, Tardigrada), two are common and widespread (Mollusca, Annelida).

Like the Cnidaria considered above, most Polyzoa (otherwise known as Ectoprocta or Bryozoa) are marine animals; just a few representatives occur in inland waters. Most inland forms are in the class Phylactolaemata, but one species (possibly two) of the Gymnolaemata are also known from Australian inland waters. The composition and regional distribution of the Australian species of the phylum are indicated in Table 7.4. Only one species listed may be endemic (*Hyalinella vahiriae*); the rest are known from at least one other continent or are regarded as cosmopolitan. *Paludicella articulata*, while it has not been found in Australia, is known from New Zealand and elsewhere and is probably present. With the exception of *Victoriella pavida*, found in the brackish regions of coastal rivers, the polyzoans of inland waters are generally confined to freshwater habitats. Here, they are most common near the sides of clear lakes, in marshes or in stream backwaters. Taxonomic knowledge of the phylum is relatively insecure, perhaps mainly because of the requirement for careful preservation of the minute adults. No modern comprehensive treatment dealing specifically with Australian forms exists.

In Australia, the Tardigrada is even less known than the freshwater polyzoans (Fig. 7.4e). All that need be noted here is that specific endemism may be quite high if the views of recent tardigrade workers are accepted. Tardigrades are minute animals (≈ 0.5 mm long), mostly found associated with submerged surfaces in fresh waters (vegetation, mud, detritus). The more typical habitat of tardigrades is the surface film on terrestrial plants.

The Phylum Mollusca stands in direct contrast to the Polyzoa and Tardigrada; its individuals are large and often conspicuous. A taxonomically important part of their body (the shell) needs little if any special means of preservation. Two important classes of the phylum occur in inland waters: the Gastropoda, with shells that are essentially helical (coiled) (Fig. 7.4g), and the Bivalvia, with shells of two separate, hinged valves (Fig. 7.4f). Considerable taxonomic confusion over species limits has arisen, and persists, involving both classes, not least because some early workers tended to describe intraspecific variants as new species. Additionally, most early taxonomists used only hard parts of the body in

Table 7.3 Turbellaria recorded from Australia.

ORDER	GENUS
Catenulida	<i>Stenostomum, Catenula</i>
Macrostomida	<i>Promacrostomum</i>
Neorhabdocoela	<i>Strongylostoma, Phaenocora, Dalyiellia, Mesostoma, Didymorchis, Bothromesostoma</i>
Alloeoocoela	<i>Prothynchus, Hofstenioplesia (?)</i>
Tricladida	<i>Eviella, Spathula, Cura, Dugesia, Romankenius, Reynoldsonia, Bdellasimilis, Neppia</i>

their determinations and ignored important details of internal structure. In any event, there is at present no comprehensive guide to the molluscan fauna of Australian inland waters. Mention should be made, however, of the useful field guide to non-marine species of southeastern Australia by Smith & Kershaw (1979) and the less detailed, but geographically wider, accounts of McMichael (1967) and Williams (1980a).

Based on these and other reference sources, some eight gastropod families can be regarded as characteristic inhabitants of Australian inland waters. A few others, more typically marine, contain species occasionally found in coastally located fresh and brackish waters. Of the eight typically non-marine families, four are operculate (Viviparidae, Hydrobiidae, Bithyniidae, Thiaridae) and four lack opercula (Lymnaeidae, Aculyidae, Planorbidae, Physidae). Space precludes detailed family discussion. The Hydrobiidae, however, is a particularly important group, with one genus, *Coxiella*, generally confined to highly saline lakes in southwestern and southeastern Australia. The Physidae includes a single species that has been introduced. The Lymnaeidae, likewise, includes two introduced species, but also has two or three native ones. Whilst none of the families is endemic in inland Australia (the indigenous Hydrococcidae is typically a coastal family), they do contain some genera and many species that are endemic. Aquatic gastropods occur in a wide variety of inland waters, from fresh to highly saline, from still to rapidly flowing. They appear to be rare in temporary fresh waters. Table 7.5 indicates the main regional patterns of distribution for the families.

Three families of the Bivalvia are unequivocally members of the Australian inland aquatic fauna and two more that are predominantly marine have species occasionally found in coastal brackish or fresh lakes. Only the truly inland families are considered further: the Hyriidae or freshwater mussels, the Sphaeriidae or pea-shell mussels and the Corbiculidae or orb-shell mussels. The mainly marine families are the Geloniidae and Mytilidae. Taxonomic knowledge of the three inland families leaves much to be desired, but from the recent work of Walker (e.g. 1981a,b) our knowledge of the ecology of some Hyriidae has greatly expanded. Within this family, confined to Australasia and South America, six genera (18 species) occur in Australia: *Velesunio* (four spp.), *Alathyria* (four), *Westralunio* (one), *Lortiella* (two), *Hyridella* (six) and *Cucumerunio* (one). Only *Lortiella* is endemic to Australia. Though freshwater mussels are common throughout most of Australia, some interesting geographical patterns occur (Fig. 7.5). Perhaps most abundant in rivers, freshwater mussels are frequently found in freshwater lakes and small bodies of predominantly permanent water. They do not occur in saline waters even though their salinity tolerance is rela-

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Table 7.4 The composition and distribution of Australian species of freshwater Polyzoa.¹ Queensland, New South Wales, Victoria and South Australia,² *Paludicella articulata* also probably occurs (see text).

SPECIES	EAST ¹	TAS.	WEST	NORTH
<i>Gymnolaemata</i> ²				
<i>Victoriella pavida</i>	+			
<i>Phylactolaemata</i>				
<i>Fredericella sultana</i>	+			
<i>Fredericella australiensis</i>	+			
<i>Plumatella repens</i>	+	+	+	
<i>Plumatella marginata</i>	+	+		
<i>Hyalinella punctata</i>		+		
<i>Hyalinella vahiriae</i>	+			
<i>Hyalinella lendenfeldi</i>	+			
<i>Stolella agilis</i>	+			
<i>Gelatinella toanensis</i>	+	+		
<i>Lophopodella carteri</i>	+			

tively high. Well-defined habitat preferences seem to be held by at least some important species. Walker's (1981a) ecological studies on the Murray River firmly indicate a division between species of the river proper (*Alathyria jacksoni*) and of waters associated with the floodplain (*Velesunio ambiguus*). Several native fish act as obligatory, albeit temporary, hosts for the glochidia larvae that are a part of the life cycle of all Australian freshwater mussels.

Less need be written about the two remaining bivalve families, in part because less is known about them. Only a single widespread genus of the Corbiculidae is known: *Corbiculina*, with some 17 species (none in southwestern Australia). Two genera of the Sphaeriidae are recognized: *Sphaerium* and *Pisidium*, with 14 described species between them. Further taxonomic investigation of these two families may reveal the need to synonymise several species. Like the Hyriidae, representatives of both families are known from a variety of fresh waters, though still or slowly flowing waters are preferred.

Representatives of the Phylum Annelida, the "true" worms and leeches, whilst perhaps not so conspicuous in inland waters as those of the Phylum Mollusca, are certainly as widespread as freshwater snails and mussels. Three classes are represented, the Polychaeta, Oligochaeta and Hirudinea. Of these, the Polychaeta, a predominantly marine group, is the rarest. A few species occur in coastally located fresh and saline lakes in southeastern Australia and there is one rarely

Table 7.5 Major regional distributions of native gastropod families of Australian inland waters. Note: most of the families also have representatives in regions outside their major regions of distribution, ¹ including, especially, Tasmania.

FAMILY	NORTH	SOUTH-WEST	CENTRAL	EAST
Viviparidae	+			
Thiaridae	+			+
Hydrobiidae				+
Bithyniidae	+		+	+
Ancylidae		+		+
Planorbidae	+	+	+	+
Lymnaeidae	+	+	+	+

recorded genus, *Stratiotrilus*, with two small (≈ 1 mm long) Australian species. Both are ectoparasites within the gill chambers of certain southeastern freshwater crayfish. The genus is known also from South America and Madagascar. Despite its great zoological interest, little is known about the biology of *Stratiotrilus*.

The oligochaetes are the most commonly encountered annelids (Fig. 7.4h). Exactly how many families should be considered within the present context is debatable. In addition to the mainly aquatic families (e.g. Naididae), there are some in which most members are terrestrial, but with a few semi-aquatic forms. Additionally, there are a few families with species recorded from Australian inland waters, but which probably have been introduced (e.g. Lumbricidae). A reasonable listing of aquatic oligochaete families present in Australian inland waters includes the Aelosomatidae, Enchytraeidae, Naididae, Tubificidae, Phreodrilidae, Lumbriculidae, Haplotaxidae, Lumbricidae and Megascolecidae. Earthworm-like, most species of these families are free-living in all manner of fresh standing or flowing waters, but a few occur in some mildly saline lakes (salinity $\approx 50 \text{ g L}^{-1}$) and two species of *Phreodrilus* are ectoparasitic on crayfish. Studies of Australian aquatic oligochaetes are in their infancy, despite the abundance and widespread distribution of the class, so that any comments on species or generic geographical distribution would be premature. The most recent comprehensive listing of Australian forms is that provided by Brinkhurst (1971; but also see Brinkhurst & Jamieson, 1971).

Relatively, the Hirudinea (leeches) have been little studied, a surprising fact given their popular fascination. All leeches have suckers which are used primarily to attach to prey (especially frogs, fishes, turtles and birds) on whose blood they feed. A few species feed on invertebrates, either by imbibing body fluids or by ingestion of whole individuals. Five families are known from Australia: the Glossiphoniidae, Ozobranchidae, Richardsonianidae, Ornithobdellidae and Erpobdellidae. Respectively, these contain four genera (two endemic), one (one), eight (six), one (none) and four (two). A total of 27 species has been recorded. Stony or vegetated regions in still or slowly flowing fresh waters are preferred habitats, but a few species are found in rapid streams. As with the Oligochaeta, any comments on the geographical distribution of Australian leeches would be premature at this time. Most records, however, relate to localities in the southeastern part of the continent and to Tasmania (see Richardson, 1967).

Arthropods: Arachnids and Crustaceans

All arthropods are characterized by the possession of an exoskeleton, a structure that obviously has proved immensely successful in an evolutionary sense, since arthropods are the most diverse, widespread and abundant of all animal groups. Most species of animals are arthropods. In terms of diversity and abundance, they dominate Australian inland waters. The following accounts of individual groups, necessarily, will be brief.

Many modern views concerning the taxonomic and phylogenetic relationships of the arthropods differ radically from views previously held. For present purposes, however, it will suffice to consider three classes of arthropods: the Arachnida, Crustacea and Insecta. This Section deals with the first two, the next one with the insects.

The class Arachnida, the spiders and mites, is mostly a terrestrial one, but two of its orders have some species associated with inland waters. The more common order is the Acarina and two of its several component groups, *viz.*, the Parasitengona and Cursaria (=Eleutherengona), have representatives in fresh waters and are known as water-mites.

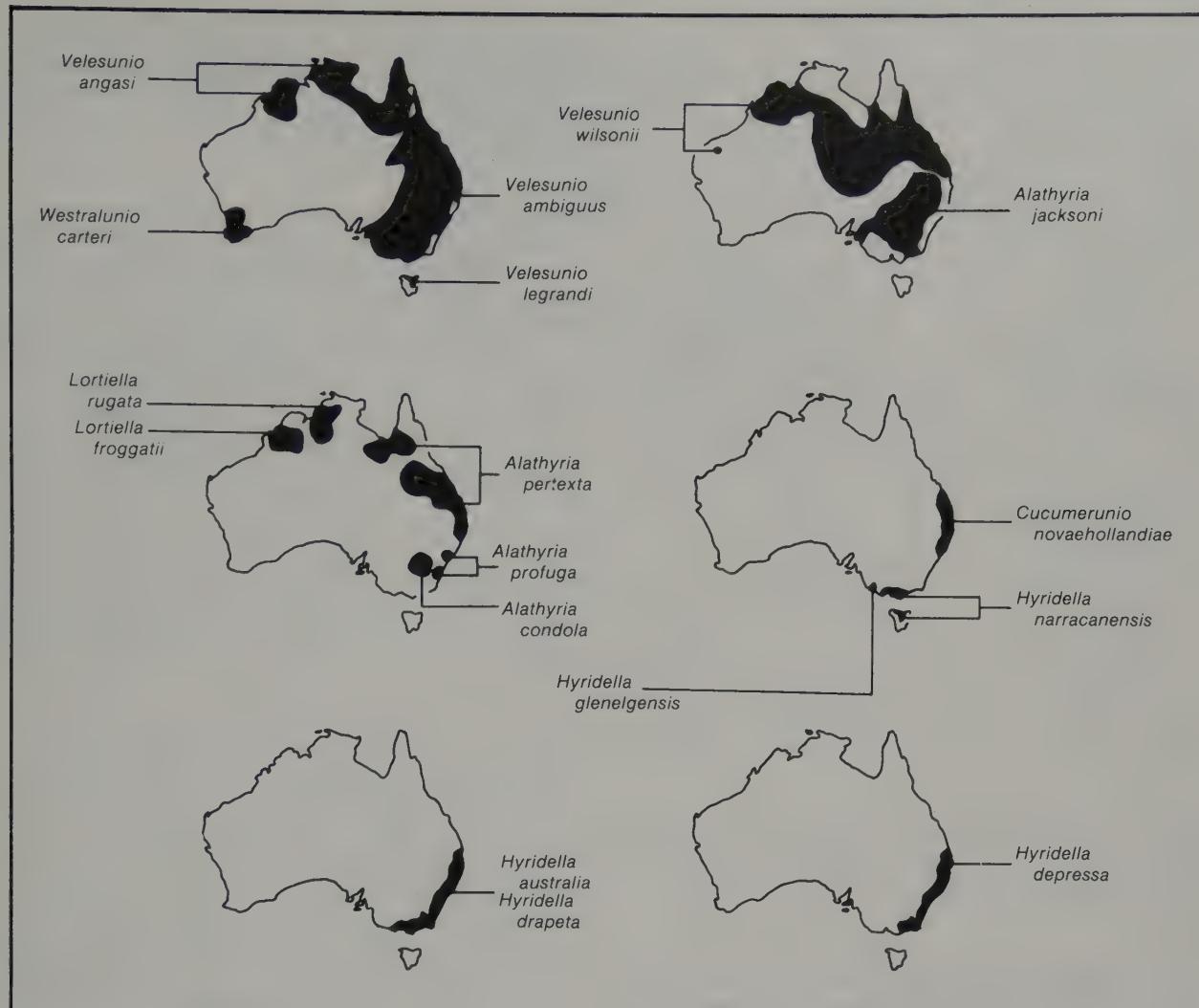


Figure 7.5 Distribution of Australian freshwater mussels. (After Walker, 1981b)

[R. Evans]

The Parasitengona contains 45 families, collectively referred to as the Hydracarina, to which belong over 60 species recorded from Australia. Many of these, as well as several genera and one family, are endemic. Only a single representative of the Cursaria is known from Australia: *Astacopsisiphagus parasiticus* in the Porohalacaridae. The less common aquatic arachnid order is the Araneae. Most of its aquatic members belong to the Pisauridae, the nursery-web or fisher spiders. A frequently encountered genus is *Dolomedes*. A few other spider families have representatives in Australia. Water-mites and aquatic spiders are most common in heavily vegetated, sheltered and shallow regions of freshwater lakes and smaller bodies of standing water, but species also occur in streams, interstitial waters and elsewhere. Water-mites include both free-living and parasitic species, but all spiders are free-living. *Astacopsisiphagus parasiticus* lives in the gill chambers of freshwater crayfish. Taxonomic knowledge concerning aquatic arachnids in Australia is accumulating slowly, largely due to the efforts of biologists domiciled on other continents. Ecological and biogeographical studies are notable for their absence.

The class Crustacea cannot be dealt with nearly so expeditiously as the Arachnida, for it is the most diverse of all animal groups and crustaceans are important invertebrates in most, if not all, inland aquatic habitats. To aid readers unfamiliar with the classification of crustaceans, Table 7.6

lists all crustacean orders found in Australian inland waters. This table also includes all crustaceans commonly found in inland waters worldwide. Only "freshwater" orders of restricted geographical distribution outside Australia (e.g. Thermostoena) or exclusively marine orders are not listed. A useful review of the Crustacea of Australian inland waters has been given recently by Williams (1981b). All major groups are illustrated by simple line drawings in Figs 7.6 & 7.7.

Anostraca. The Anostraca or fairy and brine shrimps (Fig. 7.6a) includes three families in Australia: the Artemiidae, Branchipodidae and Thamnocephalidae. A fourth family, the Streptocephalidae, is of doubtful occurrence and is not considered further. The Artemiidae contains one genus, *Artemia*, and perhaps only one species. Present evidence suggests that it has been introduced. For the most part, *Artemia* occurs in coastal salt pans associated with the production of salt. The Branchipodidae contains the endemic genus *Parartemia*, with most species occurring in southwestern Western Australia (six) and the southeast of the continent (two). The genus is also recorded from Queensland and central Australia. All species of *Parartemia* live in temporary saline waters. The Thamnocephalidae is represented by the non-endemic genus *Branchinella*, with 16 species. Generally confined to tem-

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Table 7.6 Crustacean groups found in Australian inland waters.

SUBCLASS, ORDER AND SUBORDER	COMMON NAME
'ENTOMOSTRACA'	
Branchiopoda	
Anostraca	fairy or brine shrimps
Notostraca	shield or tadpole shrimps
Diplostraca	
Conchostraca	clam-shrimps
Cladocera	water-fleas
Ostracoda	seed- or shell-shrimps
Copepoda	water-fleas
Branchiura	fish-lice
'MALACOSTRACA'	
Malacostraca	
(Division Syncarida)	
Anaspidae	-
Bathynellacea	-
(Division Peracarida)	
Amphipoda	shrimps
Isopoda	-
(Division Eucarida)	
Decapoda	prawns, crayfish, crabs

porary fresh waters, the genus is collected most frequently in arid or semi-arid regions, with species of local or wide distribution (Geddes, 1981).

Notostraca. The Notostraca or shield shrimps (Fig. 7.6b), like the Anostraca, characteristically live in temporary inland waters. Notostracans occasionally may be found, however, in more permanent waters. Two species are represented and neither occurs in highly saline waters. A reasonably distinct

Table 7.7 Amphipods of Australian inland waters. (After Williams, 1986)

FAMILY (GROUP) GENUS	NUMBER OF DESCRIBED SPECIES	GEOGRAPHICAL DISTRIBUTION
Ceinidae <i>Afrochiltonia</i>	2	southeast southwest
Eusiridae <i>Pseudomoera</i>	2	southeast
Paracalliopiidae <i>Paracalliope</i>	2	southeast
Melitidae <i>Giniphargus</i>	1	southeast
Corophiidae <i>Paracorophium</i>	1	southeast
Crangonyctoid <i>Austrogammarsus</i>	2	southeast
<i>Austrocrangonyx</i>	4	southeast
<i>Protocrangonyx</i>	1	southeast
<i>Neoniphargus</i>	10	southeast southwest
<i>Uroctena</i>	3	southwest
<i>Hurleya</i>	1	southwest
<i>Perthia</i>	2	southwest

ecological and biogeographical separation between them exists such that *Lepidurus apus viridis* (found also in New Zealand) occurs in southwestern and southeastern Australia, including Tasmania, whereas *Triops australiensis australiensis* (endemic) occurs in central and more arid parts of the continent.

Conchostraca. Like the Anostraca and Notostraca, the Conchostraca or clam shrimps (Fig. 7.6c) is predominantly found in temporary standing waters that are invariably fresh. Occasionally, conchostracans may be found in permanent fresh waters. Remarkably little is known about the taxonomy and general biology of this order, a situation probably reflecting the sporadic occurrence of populations and a distribution mainly covering the more arid and semi-arid regions of the continent and so less amenable to study. Even so, the Conchostraca is one of the most deserving of all crustacean orders awaiting the attention of freshwater biologists. The only recent studies in Australia are those of Bishop (1974) in New South Wales. Over 20 Australian species have been described, all but one endemic, in six genera: *Cyclesterheria* (one species), *Limnadopsis* (four), *Eulimnadia* (three), *Cyzicus* (eight), *Lynceus* (two) and *Limnadia* (five). The only endemic genus is *Limnadopsis*. Most genera are geographically widespread, but *Cyclesterheria* seems to be restricted to Queensland and New South Wales.

Cladocera. Though phylogenetically related to the Conchostraca, the Cladocera or water-fleas (Fig. 7.6d) stands in strong contrast to its relatives with respect to its much greater diversity and the wider variety of habitats in which it occurs. Indeed, cladocerans are amongst the most widespread, characteristic and common of all inland aquatic animals. Fresh and saline, temporary and permanent, standing and slowly flowing water provide suitable niches for water-fleas. Rapidly flowing streams and rivers do not, except in regions sheltered from the current. Six families occur in Australia and contain over 34 genera and about 125 species. The exact number of species depends upon the credence given to recent taxonomic revisions. According to the latest comprehensive revision (Smirnov & Timms, 1983), the division of species amongst the families is as follows: Sididae (five species), Chydoridae (68), Macrothricidae (two), Moinidae (six), Bosminidae (two) and Daphniidae (23). Note that while the species numbers listed need minor revision in the light of recent work on particular genera, the numbers do indicate the structure of diversity between the families. A few genera and many species (>40) are endemic. On the other hand, a few cosmopolitan genera and species have been recorded. Four families important outside Australia, the Holopедidae, Polypheidae, Cercopagidae and Leptodoridae, are not represented here. The paucity of available data precludes any firm statements concerning the geographical distribution of Australian Cladocera.

Ostracoda. The Ostracoda, seed- or shell-shrimps (Fig. 7.6e), is almost as ubiquitous and diverse as the Cladocera. All manner of inland aquatic habitats (except rapidly flowing streams) support ostracods and some 100 Australian species have been described. Unlike the Cladocera, however, not all ostracods are free-living. Species of the Entocytheridae are commensal upon freshwater crayfish. Of particular note amongst the free-living ostracods are those living in highly saline lakes; they include many species, several extremely tolerant to elevated salt concentrations. Ostracods are not nearly so important in salt lakes on other continents. Those present in Australian salt lakes have been reviewed recently by De Deckker (1981). Nine families contain the species recorded from all inland aquatic situations in Australia: Limnocytheridae, Entocytheridae, Cytheromatidae, Cytherideidae,

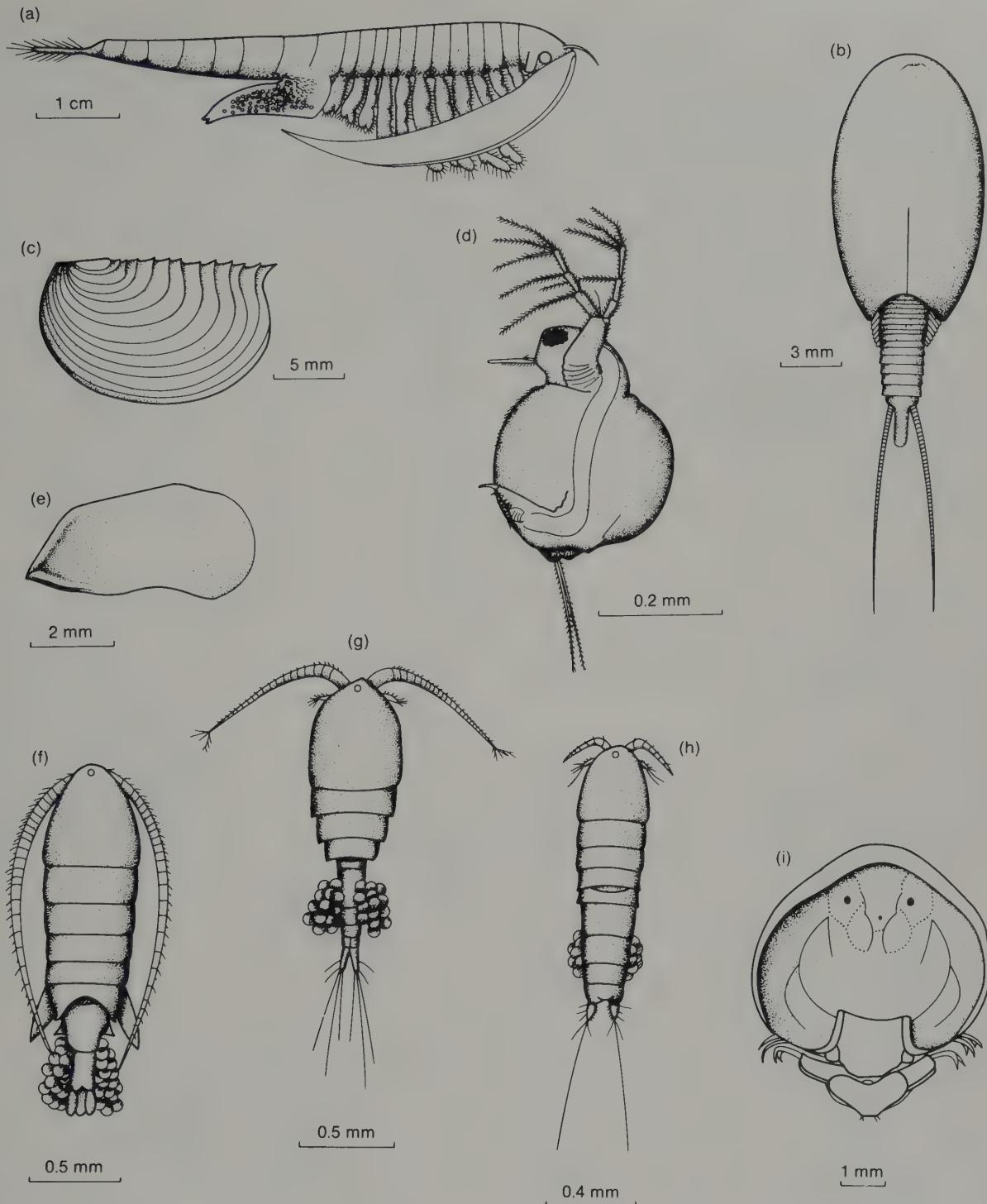


Figure 7.6 Australian freshwater entomostracan Crustacea. (a) *Branchinella* (Anostraca); (b) *Lepidurus* (Notostraca); (c) *Limnadopsis* (Conchostraca); (d) *Moina* (Cladocera); (e) *Mytilocypris* (Ostracoda); (f) ovigerous female of *Boeckella* (Copepoda, Calanoida); (g) ovigerous female of *Microcycllops* (Copepoda, Cyclopoida); (h) ovigerous female of *Attheyella* (Copepoda, Harpacticoida); (i) *Dolops* (Branchiura). (After Williams, 1983a) [R. Evans]

Darwinulidae, Ilyocyprididae, Candonidae, Cyprididae and Cypridopsidae. The last four account for most species and both endemic and cosmopolitan forms are represented. Much of our taxonomic knowledge is due to the work of P. De Deckker (e.g. 1983). With regard to geographical distributions, some general patterns can already be discerned at this early stage of knowledge. A few species appear restricted to the north (e.g., *Hemicypris*). A larger number appears restricted to southern regions. Several forms appear to occur

throughout the continent (e.g., *Newnhamia fenestrata*). Distributions of a reasonably large number are essentially local in nature.

Copepoda. The Copepoda (Fig. 7.6f,g,h) includes both free-living and parasitic forms, but the former are more important and better known. The most notable parasitic species appears to be *Lerneia cyprinacea*, a member of the Lernaeopodoida and an ectoparasite of several species of both native and

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introduced freshwater fish in southeastern Australia. The free-living copepodan orders are the Calanoida, Cyclopoida and Harpacticoida. All are well represented in Australia, with many species in fresh and saline, temporary and permanent, standing and slowly flowing waters throughout the continent. Within the Calanoida, five genera are known, only two of which occur outside Australasia, *viz.* *Diaptomus* and *Boeckella*. The most diverse genera are *Boeckella* (≈ 20 species) and *Calamoecia* (≈ 12); most of the species are endemic. A few calanoid species are widespread (e.g. *Boeckella triarticulata*, *Calamoecia lucasi*), but most have distributions more or less geographically restricted. *Diaptomus*, with two species, is restricted to the northern half of the continent. Some recent work suggests that similar patterns of endemism and distribution may well be shown by the Cyclopoida, a group once thought to have many more cosmopolitan species than now appears to be the case. Important genera of cyclopoids in Australia include *Mesocyclops*, *Halicyclops* and *Microcyclops*. Little can be said of the more cryptic Harpacticoida other than to note that the species most frequently encountered in fresh waters is *Attheyella australica* and in inland saline waters is *Mesochra baylyi*. Recent works on Australian copepods include Bayly (1984), Morton (1985) and Hamond (1971).

Branchiura. The Branchiura or fish-lice (Fig. 7.6i) is allied to the Copepoda, and includes a small number of species ectoparasitic on frogs or, more usually, fishes. Two genera have been recorded, neither of which is endemic: *Argulus* has three species, at least two probably introduced, and *Dolops* has a single endemic species, *D. tasmanianus*, an ectoparasite of certain galaxiid fish in Tasmania.

Crustaceans generally larger than those just discussed and members of the Subclass Malacostraca include the syncarids, amphipods, isopods and decapods. Most are confined to fresh and usually permanent waters, both standing and flowing, but a few amphipods and isopods can resist desiccation and tolerate relatively high salinities.

Syncarida. From a phylogenetic viewpoint, the Syncarida is particularly interesting in that one of its orders, the Anaspidae, includes forms which probably are morphologically close to the ancestor of all malacostracans. The most famous example is *Anaspides tasmaniae* (Fig. 7.7b), now confined to small streams in Tasmania. Formerly, it seems, it also lived in Tasmanian lakes. Recent investigations have revealed a much greater diversity of anaspidaceans than was thought to be the case, including many forms of scarcely less interest than *Anaspides*. Successful collections have been made at several localities on the eastern side of the continent as well as from many places in Tasmania. To date, four families accommodate collected material: Anaspidae, Koonungidae, Psammaspidae and Stygocarididae. Of these, only the stygocarids are found outside Australia (New Zealand and South America). All described forms of anaspidaceans are endemic. The other order of the syncarids found in Australia is the Bathynellacea (Fig. 7.7a), a group of cosmopolitan distribution. All members are blind, small and either subterranean or interstitial in habit. Their extreme morphological reduction, a clear adaptation to their habitat, makes them of far less interest to phylogeneticists than their anaspidacean relatives. About 10 species in five genera have been described from Australia.

Apart from *Anaspides tasmaniae*, which occurs widely in Tasmania, most Australian syncarids appear to have restricted distributions. Notable contributions to our knowledge of this group of crustaceans have been made by Lake *et al.* (1974) and Schminke (1975).

Amphipoda. Australia seems to have been a major evolutionary centre and refuge for the Amphipoda (Fig. 7.7f), one of several crustacean groups popularly called freshwater shrimps. At least six family groups have been delimited for Australian freshwater species: ceinids, eusirids, paracaliliopids, melitids, corophiids and crangonyctoids. Most of the species involved seem to have evolved from marine ancestors, but the crangonyctoids, and perhaps the corophiids, appear to have descended from ancient Gondwanan forms. The greatest diversity is found in Tasmania where amphipods are ubiquitous in almost all permanent freshwater lakes, rivers and streams. On the mainland, amphipods are most abundant and diverse in the southwest and southeast, especially in upland areas. One genus, *Afrochiltonia* (formerly *Austrochiltonia*), is of wider occurrence and is found throughout southern Australia in both fresh and mildly saline (<30 g L⁻¹ salinity) waters. The taxonomy of the group has yet to be placed upon a firm footing, but an indication of the current formal situation with regard to generic and specific numbers is given in Table 7.7. This Table also shows the general geographical pattern. Important modern references to Australian forms are made in the compilation of Barnard & Barnard (1983) on freshwater amphipods. Australian subterranean species are referred to briefly by Williams (1986).

Isopoda. The Isopoda (Fig. 7.7c,d,e), for which there is no collective popular name, includes a wider diversity of forms than the Amphipoda, but, like this group (to which they are related), most inhabit permanent and fresh water. Even so, quite a wide variety of habitats support isopods in Australia. Coastal lakes and the freshwater reaches of estuaries in eastern Australia are inhabited by *Cymodetta* and anthurids (Table 7.8). Streams, pools and freshwater lakes support *Heterias*, *Pseudasellus* and many species of phreatoicid. Salt lakes, both permanent and temporary throughout southern Australia, frequently contain *Haloniscus searlei*. Mound springs in central desert regions often have dense populations of phreatoicids. Moreover, whilst all amphipods and most isopods are free-living, one isopod, *Astroargathona*, is an ectoparasite of decapod prawns in eastern rivers. With the exception of *H. searlei*, the geographical distributions of individual species are limited. Many phreatoicid species, for example, are known from only a single locality. The Great Lake of Tasmania stands out in this respect. Table 7.8 summarizes the overall composition of the Australian isopod fauna. Note that all described genera are endemic. As the table indicates, by far the most diverse group is the Phreatoicidea. It contains about 40 described species and 17 genera. A predominantly Gondwanan group, the phreatoicids are also known from India, New Zealand and South Africa. The group, however, attains its greatest diversity and abundance in Australia. Work on Australian isopods (see especially Nicholls, 1943; 1944) has been concerned almost exclusively with phreatoicid taxonomy and is now some 40 years old. A modern taxonomic revision of the phreatoicids, as well as comprehensive studies of other isopods, is overdue. The biology of *Haloniscus* has been reviewed recently by Williams (1983b).

Decapoda. The order Decapoda is even more diverse in morphology than the Isopoda and species range from rather small, slender, swimming atyid prawns to large, robust, bottom-living crayfish. It is also more diverse in a taxonomic sense than the Isopoda or, indeed, any other malacostracan order, as Table 7.9 demonstrates. The Atyidae (Fig. 7.7g) is found throughout northern and eastern Australia, including Tasmania, mostly in lowland rivers, farm dams, billabongs and at the sheltered edges of lakes. Additionally, particular species inhabit certain caves in the Northern Territory and at North West Cape in Western Australia. One genus is confined to fast flowing streams on the eastern coast. Atyids cannot resist desiccation, so that all species are found only in

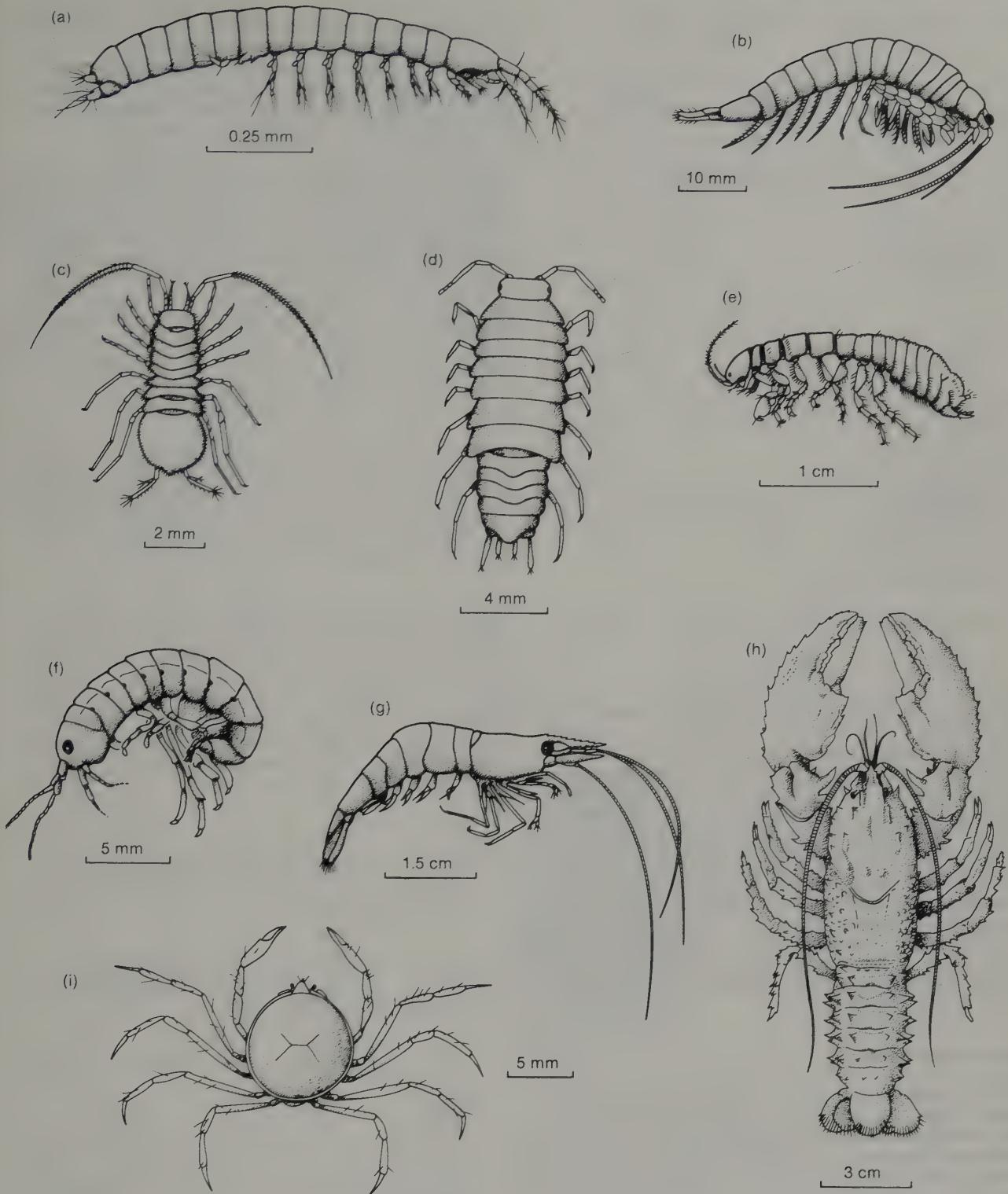


Figure 7.7 Malacostran crustaceans of Australian inland waters. (a) *Bathynella* (Syncarida, Bathynellacea); (b) *Anaspides tasmaniae* (Syncarida, Anaspidacea); (c) *Heterias* (Isopoda, Janiridae); (d) *Haloniscus searlei* (Isopoda, Oniscidae); (e) *Metaphreatoicus australis* (Isopoda, Phreatoicidae); (f) *Afrochiltonia* (Amphipoda); (g) *Paratya australiensis* (Decapoda, Atyidae); (h) *Euastacus armatus* (Decapoda, Parastacidae); (i) *Amarinus lacustris* (Decapoda, Hymenosomatidae). (After Williams, 1983a) [R. Evans]

more or less permanent bodies of water. The slightly more robust palaemonid prawns have a wider geographical distribution than the atyids and are found throughout the eastern half of Australia (except in the southeastern corner and in Tasmania) and in northern regions. One genus, *Palaemonetes*, is found only in the far southwestern region. The Palaemonidae also live in a wide variety of permanent

fresh waters. An even wider variety of habitats is occupied by the Parastacidae or crayfish (Fig. 7.7h) (local names include yabbies, marron and gilgies). In fact, the family includes some forms which at best can be regarded only as semi-aquatic. Thus, in addition to many sorts of permanent fresh waters, temporary water may also support parastacids. As a result, species of *Cherax*, geographically the most widespread

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Table 7.8 Isopods of Australian inland waters,¹ including Tasmania, according to Nicholls (1943, 1944),² see Timms (1973).

SUBORDER, FAMILY AND GENUS	NUMBER OF DESCRIBED SPECIES	DISTRIBUTION
Flabellifera		
Cirolanidae		
<i>Astroargathona</i>	1	east
Sphaeromatidae		
<i>Cymodetta</i>	1	east
Asellota		
Janiridae		
<i>Heterias</i>	2	southeast ¹
<i>Pseudasellus</i>	1	Tasmania
Oniscoidea		
Oniscidae		
<i>Haloniscus</i>	2	south ¹
Phreatoicidae ²		
Amphisopidae (10 genera)	14	widespread
Phreatoicidae (7 genera)	25	southeast ¹
Anthuridea		
not determined ³		

genus, may be found in quite arid areas. The next most widespread genus is *Euastacus*, found in the southeast, but all other genera have restricted distributions. A noteworthy feature of parastacid distribution in general is that the family is confined to the land-masses of the Southern Hemisphere. Of crabs found in Australian inland waters, three families rate at least passing mention. The Sundatophilusidae has two species of *Holthuisiana* in northern fresh waters (again, often in rather arid areas). The Hymenosomatidae is represented by *Amarinus lacustris* (Fig. 7.7i) in slightly saline southeastern waters. The Grapsidae is represented by a semi-terrestrial species, *Leptograpsodes octodentatus*, found in fresh and brackish coastally located waters. An introduction to the literature on decapods of Australian inland waters may be gained from the bibliographies of Williams (1980a; 1981b).

Arthropods: Insects

Aquatic insects are a major component of the fauna of aquatic ecosystems, particularly in streams, where they usually predominate. About thirteen orders of insects have some aquatic members and all are represented in Australian inland waters (Williams, 1981c). Fig. 7.8 illustrates several examples.

In five orders, all species have aquatic or semi-aquatic larvae and terrestrial adult stages. Included here are the Ephemeroptera (mayflies), Plecoptera (stoneflies), Trichoptera (caddisflies), Odonata (dragonflies and damselflies) and Megaloptera (alderflies). All are relatively small orders by comparison with other insect orders; their larvae, nevertheless, may be extremely abundant in aquatic habitats.

A further three orders have only a small proportion of aquatic species, but these species are commonly encountered and often abundant. Included here are the Diptera (two-winged flies), some species of which have aquatic larvae and the Coleoptera (beetles) and Hemiptera (bugs), in which either adults or larvae or both may be aquatic.

Four other orders have a small proportion of comparatively rarely encountered species with aquatic larvae: the Mecoptera (scorpion flies), Neuroptera (lacewings), Lepidoptera (moths and butterflies) and Hymenoptera (wasps, ants and bees). The Collembola (springtails) is a group of microarthropods, often grouped with insects, which has a number of species commonly found associated with water surface films.

The distribution of aquatic insects is determined by several factors, including the present and past distribution of aquatic habitat as well as the evolutionary history and dispersal ability of the particular species. Temporary lakes and streams are inhabited only by species which can withstand drying or which can recolonize from refugia during wet periods. Both types are known amongst the Australian aquatic insects. Drought resistant stages are recorded in the Trichoptera (Towns, 1983), Plecoptera (Towns, 1983; 1985; Yule, 1985) and Coleoptera (Smith & Pearson, 1985). Because of their flight abilities, the Hemiptera, Coleoptera and Odonata are common early colonizers of temporary waters.

Overall, four zoogeographic components can be recognized: Gondwanan, northern tropical/Asian, unique Australian and cosmopolitan. Most aquatic insects are to be found along the eastern coast and in Tasmania, the Gondwanan component most abundantly in the south and the Asian/tropical component more abundantly in the north.

Ephemeroptera. The order Ephemeroptera contains 20 families worldwide (Hubbard & Peters, 1976), of which seven occur in Australia (Table 7.10). Compared to the rest of the world, the Australian mayfly fauna has several unusual features. The first is the strong dominance of the Leptophlebiidae (Table 7.10). This dominance, likely to increase as further taxonomic work is carried out (Campbell, in press), contrasts strongly with the situation in the rest of the world, North America in particular (Table 7.11). The Baetidae

Table 7.9 Decapods of Australian inland waters,¹ only major genera of Atyidae and Parastacidae given; ² including Tasmania; ³ not including Tasmania; ⁴ a few species widespread, but many with more or less restricted distributions.

FAMILY GENERA ¹	NUMBER OF DESCRIBED SPECIES	DISTRIBUTION
Atyidae		
<i>Paratya</i>	1	east ²
<i>Caridina</i>	6	north, east ³
+ 4 others	6	north, west, east ³
Palaemonidae		
<i>Macrobrachium</i>	9	north, central, east ³
<i>Palaemonetes</i>	1	southwest
Parastacidae		
<i>Cherax</i>	27	widespread ⁴
<i>Euastacus</i>	28	widespread ⁴
<i>Engaeus</i>	24	widespread ⁴
+ 7 others	≈ 25	widespread ⁴
Hymenosomatidae		
<i>Amarinus</i>	1	southeast
Sundatophilusidae		
<i>Holthuisiana</i>	2	north, central
Grapsidae		
<i>Leptograpsodes</i>	1	southeast, southwest

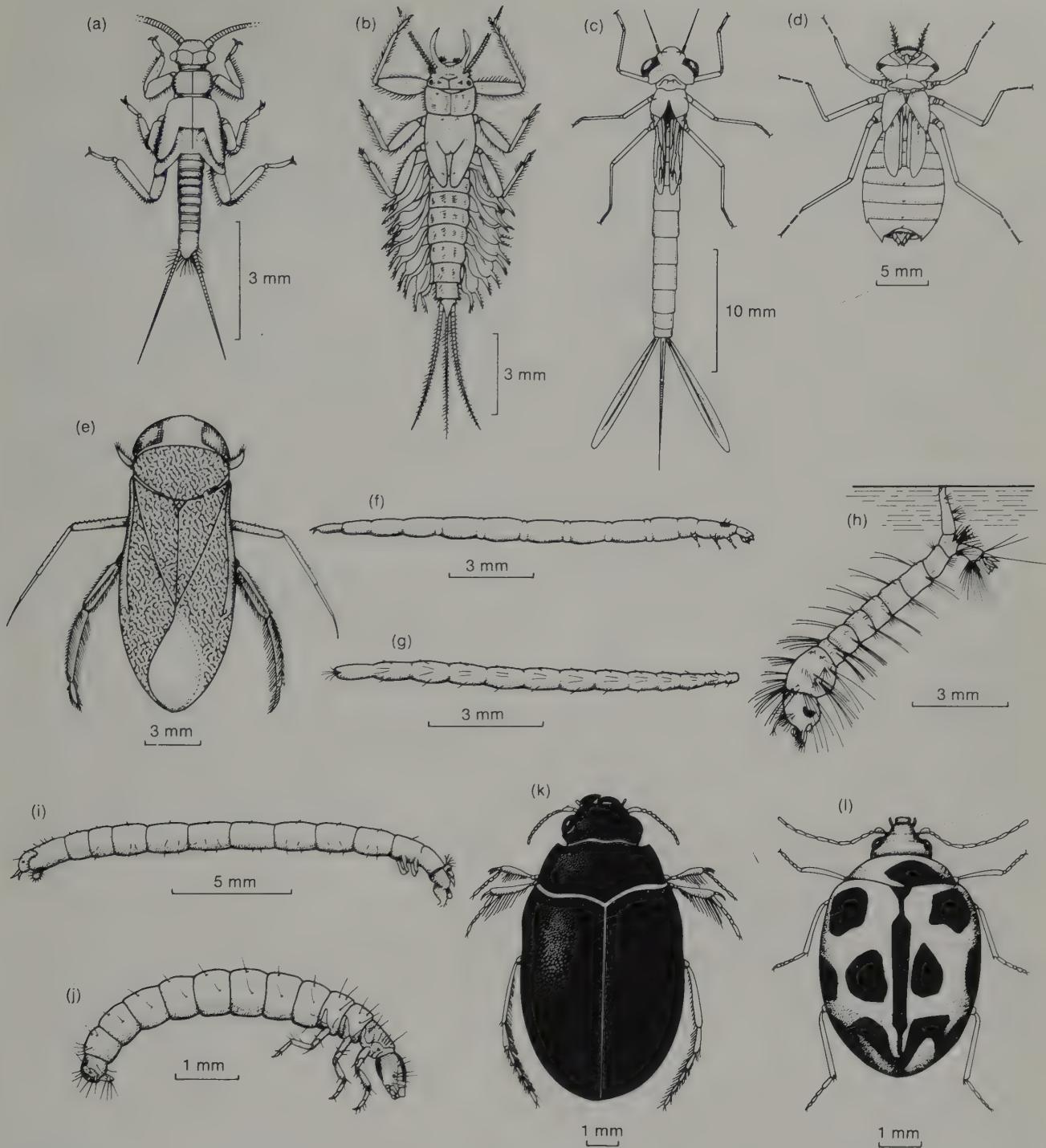


Figure 7.8 Some Australian aquatic insects. (a)–(d), (f)–(j) are nymphal or larval forms; (e), (k) and (l) are adults. (a) *Dinotoperla fontana* (Plecoptera); (b) *Jappa* (Ephemeridae); (c) *Caliagrion billinghami* (Odonata); (d) *Hemicordulia australiae* (Odonata); (e) *Agraptocorixa eurynome* (Hemiptera, Corixidae); (f) *Nannochorista* (Mecoptera); (g) *Culicoides* (Diptera, Ceratopogonidae); (h) culicid (Diptera, Culicidae); (i) *Chironomus* (Diptera, Chironomidae); (j) *Agapetus* (Trichoptera); (k) *Hygrobia* (Coleoptera); (l) *Macrohelodes* (Coleoptera). (After Williams, 1983a)

[R. Evans]

forms a significant part of the Australian fauna, as elsewhere, but the absence of the Heptageniidae and the Tricorythidae is a notable feature.

Given the poor state of taxonomic knowledge of Australian mayflies, it is difficult to be certain about the level of endemism of the fauna. About 75% of the genera and a higher proportion of the species appear to be indigenous. The Australian leptophlebiids have undergone an extensive radiation and appear to occupy niches filled elsewhere by other fam-

ilies. Thus, *Kirrara procera* and *Deleatidium pusillum* have similar nymphs to some North American Heptageniidae (Campbell & Peters, 1986) and nymphs of *Jappa* resemble certain European and North American Ephemeridae.

The distributional patterns of the Australian mayflies reflect both the distribution of permanent water (on which most species depend) and their evolutionary histories. The fauna can be split into three groups based on apparent evolutionary affinities and the distribution of related groups. The first has

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Table 7.10 Composition of the ephemeropteran fauna of Australian inland waters.

FAMILY	NUMBER OF GENERA	NUMBER OF SPECIES
Caenidae	1	5
Baetidae	5	11
Ephemerellidae	1	1
Prosopistomatidae	1	1
Siphlonuridae	3	7
Oligoneuriidae	1	3
Leptophlebiidae	9	43

Table 7.11 Composition of the six largest families of mayflies, North America and Worldwide. (After Hubbard & Peters, 1976; Edmunds et al., 1976; Merritt & Cummins, 1980)

FAMILY	NUMBER OF GENERA (AND SPECIES)	
	North America	Worldwide
Baetidae	10 (128)	17 (519)
Heptageniidae	12 (152)	28 (378)
Leptophlebiidae	8 (70)	62 (377)
Siphlonuridae	8 (81)	26 (163)
Ephemerellidae	1 (85)	7 (163)
Tricorythidae	2 (21)	13 (122)

amphinotic or transantarctic affinities with relatives in South America and New Zealand. The second has tropical affinities. The third component consists of cosmopolitan groups.

The Australian members of the Siphlonuridae, Oligoneuriidae and Leptophlebiidae appear to have their closest relatives in South America. The first two families are restricted to permanent streams and lakes in eastern Australia and are most abundant in the southern half of the continent (Campbell, 1986). Of the four genera involved, *Ameletoides* (Siphlonuridae) has been recorded no further north than Mt Kosciusko, *Coloburiscoides* (Oligoneuriidae) is distributed as far north as the northern edge of the southern tablelands of New South Wales, *Tasmanophlebia* (Siphlonuridae) extends as far north as Barrington Tops in northern New South Wales and only *Mirawara* (Siphlonuridae) extends into Queensland, where it occurs at least as far north as Cairns.

Table 7.12 Composition of the plecopteran fauna of Australian inland waters. Based on various sources but including Theischinger (1984, 1985), Yule (1984) and Zwick (1979a).

FAMILY	NUMBER OF GENERA	NUMBER OF SPECIES
Notonemouridae	6	19
Austroperlidae	5	7
Eustheniidae	3	10
Gripopterygidae	10	88

Of interest is that the limits of distribution of *Coloburiscoides* and *Tasmanophlebia* correspond to regions of discontinuity in the distributions of a number of other orders of aquatic insects (cf. Watson & Theischinger, 1984). Curiously, neither *Mirawara* nor *Coloburiscoides* occurs in Tasmania, although both are common in streams of the Great Dividing Range in Victoria. Since both genera occur on the mainland at altitudes above 1,000 m, it would appear unlikely that they were eliminated by low temperatures during Pleistocene glaciations. Both genera have their closest relatives in South America and New Zealand, indicating that they were present in Australia well before the separation of Tasmania from the mainland. Both *Ameletoides* and *Tasmanophlebia* occur in Tasmania.

The Australian Leptophlebiidae have been placed in the subfamily Atalophlebiinae by Peters (1980). Pescador & Peters (1980) have suggested that all known genera of cool-adapted South American leptophlebiids have their closest relatives in Australia. This suggests a Gondwanan origin for the group. Although leptophlebiids occur in temporary streams (Suter, 1980; Marchant, 1982) and lakes, most Australian species have been recorded from the streams of the Great Dividing Range in eastern mainland Australia or from Tasmania. Several species are common in streams in the southwest of Western Australia.

Two families of Australian mayflies, the Prosopistomatidae and the Ephemerellidae, appear to have northern affinities. Both are represented by single species recorded only from northeastern Australia and, in the case of the prosopistomatids, the species also occurs in New Guinea.

Both the Baetidae and Caenidae are cosmopolitan families, although both are absent from New Zealand (Wise, 1977). Only a single caenid genus, *Tasmanocoenis*, is present and it is widespread and apparently endemic (Suter, 1984). The Baetidae is a larger family in Australia. Five genera are recorded and one, *Bungona*, is endemic. There are undoubtedly further species and probably genera of this family to be described. At present, little can be said other than that the family is common and widespread in Australian inland waters.

Plecoptera. A small order, the Plecoptera or stoneflies contains about 2,000 species in world total (Zwick, 1981c). The larvae are aquatic and most abundant in cool, upland streams (Hynes, 1976). About 125 species have been described from Australia. A new genus and 39 new species have been described since the review by Zwick (1980). Only four families are present in Australia (Table 7.12). All four are restricted to the Southern Hemisphere and all genera but one are endemic (Illies, 1965). The Gripopterygidae dominates, accounting for about 70% of described species (Table 7.12).

In his recent higher classification of the Plecoptera, Zwick (1980) recognizes two suborders, the Antarcticoperlaria and the Arctoperlaria. Three of the Australian families are placed in the first suborder, which is thought to have had a Gondwanan origin (Zwick, 1981c). The other family, the Notonemouridae, appears to be derived from Northern Hemisphere ancestors, but its exclusively Southern Hemisphere extant distribution and its restriction in Australia to the cool southeastern corner of the continent indicate that it is not a recent arrival.

Diversity is greatest in the southeastern corner of the mainland and Tasmania. Four species are known from southwestern Western Australia (Hynes & Bunn, 1984), only three of which have been described. All four are gripopterygids. The three described species are endemic species of genera previously described from eastern Australia. Hynes & Bunn (1984) suggest that they are not related particularly closely to their congeners. The fourth (undescribed) species is related

closely to, if not identical with, *Dinotoperla bassae*, a species known from temporary ponds and lowland streams in Victoria and Tasmania (Hynes & Bunn, 1984). While further stonefly species may be described from the southwest, the number is unlikely to be large.

Similarly, the plecopteran fauna of northeastern Australia, while poorly known, is apparently not very diverse (Zwick, 1981c). The eustheniid *Stenoperla australis* occurs north of Cairns and the monotypic gripopterygid genus *Kirrama* and four species of *Leptoperla* are apparently endemic in this region (Theischinger, 1981).

The stoneflies of Tasmania appear to be highly endemic at the species level, with a single endemic genus, *Cardioperla*. Hynes & Hynes (1980) note that only five or six of the Tasmanian species are also present on the mainland. More recent taxonomic studies (Hynes, 1982) have confirmed that only six out of 60 described Tasmanian species are also present on the mainland. Since there are several more undescribed species endemic to Tasmania (Hynes, 1982), the final level of species endemism will exceed 90%. Apparently, the land connections between Tasmania and the mainland, which have existed several times since the Pleistocene, did not provide suitable habitat for most stoneflies. Curiously, the eustheniid genus *Stenoperla*, which occurs along the entire length of the east coast of Australia and in New Zealand, is not present in Tasmania – a pattern of distribution similar to that of *Mirawara* and *Coloburiscoides* (Ephemeroptera).

Trichoptera. Studies of the Australian Trichoptera or caddisflies are patchy. The fauna of some geographical areas (e.g. Tasmania) and families (e.g. Hydroptilidae; Wells, 1979) is well known, while knowledge of the rest of the fauna is poor. The Australian fauna contains about 405 described species, placed in 91 genera and 24 families (Neboiss, 1983). Half the described species, however, belong to three families: the Hydrobiosidae, Hydroptilidae and Leptoceridae (Table 7.13).

About two-thirds of all trichopteran families are known from Australia (Williams, 1980a). One, the Plectrotarsidae, is endemic. The Australian fauna is distinctive in that the Limnephilidae constitutes less than 1% of the Australian species and yet is abundant in the Northern Hemisphere. It comprises about 25% of the North American fauna (Merritt & Cummins, 1978). The leptocerids, on the other hand, are apparently more abundant in Australia than elsewhere. Most species and genera of Australian caddisflies are endemic.

The Australian Trichoptera include three zoogeographic groups: one with southern relationships, another with northern relationships and a third endemic group (Ross, 1967; Winterbourn, 1980). The group with northern origins includes some hydropsychids, leptocerids, philopotamids and glossosomatids, as well as the Apsilochoreminae (Hydrobiosidae) (Neboiss, 1977). These are considered comparatively recent arrivals and to have entered Australia via Asia and New Guinea (Winterbourn, 1980).

Recent studies have shown that transantarctic relationships in the Trichoptera are stronger than originally thought (*cf.* Riek, 1974). Ross (1967) previously had noted these for the leptocerid subfamily Triplectidinae and some hydropsychids, notably the genus *Smicrophylax*. Neboiss (1977) suggests that the Hydrobiosinae (Rhyacophilidae) and the small families Kokiriidae, Oeconesidae, Tasimiidae, Calocidae, Helicophidae, Conoesucidae and Philorheithridae have transantarctic distributions. All are cool-adapted forms most abundant in southeastern mainland Australia and Tasmania.

Table 7.13 Composition of the trichopteran fauna of Australian inland waters. (After Neboiss, 1983)

FAMILY	NUMBER OF GENERA	NUMBER OF SPECIES
Hydrobiosidae	15	57
Glossosomatidae	1	8
Hydroptilidae	14	80
Philopotamidae	2	18
Stenopsychidae	2	9
Hydropsychidae	8	28
Polycentropodidae	6	12
Ecnomidae	2	22
Chathamiidae	1	1
Tasimiidae	2	6
Limnephilidae	1	3
Oeconesidae	1	1
Kokiriidae	3	4
Plectrotarsidae	3	5
Conoesucidae	6	21
Antipodocciidae	1	1
Calocidae	3	9
Helicophidae	2	6
Odontoceridae	2	4
Atriplectididae	1	1
Philorheithridae	5	13
Helicopsychidae	2	6
Calamoceratidae	1	10
Leptoceridae	14	80

The unusual marine family Chathamiidae, represented by a single species in both southeastern Australia and New Zealand (Neboiss, 1983), and the sole Australian endemic family, Plectrotarsidae, appear to have arisen in the Australian Region (Riek, 1970a).

Like the Ephemeroptera and Plecoptera, the greatest diversity occurs in the southeastern part of the mainland and in Tasmania. All 24 families have been recorded from this region (Neboiss, 1981). Unlike the previous two orders, however, trichopterans are far more widespread. Ten to 15 species from some four families occur in arid, central Australia. Tasmanian trichopterans are also highly endemic, with 74% of species known from nowhere else (Neboiss, 1977). In the southwest of Western Australia, 43 species have been recorded, of which about 70% are restricted to the region (Neboiss, 1981).

Odonata. Similarities and differences between the odonatan fauna of Australia and of some other regions are summarized by Watson (1981). The Australian fauna is highly endemic at both the generic (44%) and specific (74%) levels. There are a number of archaic groups, including the endemic families Hemiphlebiidae and Lestoideidae and the subfamilies Chorismagrioninae (Chlorolestidae) and Cordulephyinae (Corduliidae) (O'Farrell, 1970). Sixteen families are represented, including 99 genera and about 269 species (Table 7.14). Compared with North America, the families Gomphidae and Coenagrionidae are relatively less important in Australia (11% vs. 21% and 11% vs. 23% of total species, respectively), whilst the Aeshnidae is relatively more important (14% vs. 9%).

Like trichopterans, the Odonata fall into three groups with respect to evolutionary affinities. About 35% of species belong to groups with southern distributions (Watson, 1981). Of these, the Chlorolestidae, the neopetaline Aeshnidae and the small gomphids have clear Gondwanan origins (Watson, 1981; Watson & O'Farrell, 1985). A second group, including the gomphomacromine Corduliidae and the brachytronine

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Aeshnidae, does not have an obvious link with Gondwana (though with a broadly southern distribution). Another 37% of species belongs to groups with clear northern affinities (Watson, 1981). The entire families Coenagrionidae and Libellulidae are in this category, together with parts of some eight other families represented in Australia. Finally, there are six Australian genera whose affinities are not yet clear.

The larvae of dragonflies and damselflies can survive in a wide range of aquatic habitats. They are common in both standing and running waters. In southern Australia at least, a relatively higher proportion of species occurs in streams (40%) than appears to be the case elsewhere (Watson, 1981). A surprisingly large number of species occurs in temporary waters. Species survive by means of drought resistant eggs or larvae or, more commonly, by rapid life histories and strong dispersal abilities. A few species can survive in moderately saline water. There is at least one with a terrestrial larva which lives in the leaf-litter of rainforests (Watson, 1981).

Like the three previous orders discussed, diversity is greatest along the eastern coast. Unlike the previous orders, however, the largest number of species occurs in the northeast. Some 137 species occur in northeastern Queensland, compared with only 65 in Victoria. Odonatans are generally abundant in tropical waters and the fauna of New Guinea is far richer than Australia. In general, the Gondwanan element in the Australian fauna is cool-adapted and most abundant in the south, whilst the northern fauna has tropical affinities.

Watson & Theischinger (1984) note four regions of taxonomic disjunction in eastern Australia based primarily on odonatan distributions, but also on other aquatic insects as well, particularly the Plecoptera and Megaloptera. Three of these disjunctions break the eastern coast into four biogeographic regions. One disjunction, the gap between the Petaluma Range and Eungella, separates the fauna of northern Queensland from that further south. The second break occurs at the southern margin of the northern tablelands of New South Wales and a third at the northern limit of the southern highlands. Watson & Theischinger also suggest that Carnarvon Gorge, a site in southeastern Queensland with permanent water in an area where rainfall is low and surface water usually only temporary, seems to form a biogeographic island.

Table 7.14 Composition of the odonatan fauna of Australian inland waters. (After Watson, 1981)

FAMILY	NUMBER OF GENERA	NUMBER OF SPECIES
Protoneuridae	8	23
Lestoideidae	1	2
Coenagrionidae	13	30
Megapodagrionidae	2	15
Lestidae	3	14
Chlorolestidae	3	8
Hemiphlebiidae	1	1
Amphipterygidae	1	4
Chlorocyphidae	1	1
Calopterygidae	1	1
Gomphidae	6	30
Petaluridae	1	4
Aeshnidae	16	38
Synthemidae	4	16
Corduliidae	12	30
Libellulidae	26	52

Megaloptera. The Megaloptera, or alderflies, is a small order with carnivorous aquatic larvae and flying adults. The Australian fauna contains both of the two described families (Riek, 1970b). The Sialidae is represented by two endemic genera, *Austrosialis* and *Stenosialis*, each with two species. *Austrosialis ignicollis* is the sole megalopteran species from Tasmania, to which it is restricted. The other three sialids occur in streams along the eastern coast of the mainland. The Corydalidae is represented by two genera: *Protochaulioides* with two species and *Archichaulioides* with 18 (Theischinger, 1983). *Protochaulioides* is also recorded from North and South America, while *Archichaulioides* has a Gondwanan distribution. Curiously, the latter genus does not occur in Tasmania. It is found from Victoria to Queensland and in New Zealand, a distribution similar to that of the ephemeropteran genera *Coloburiscoides* and *Mirawara* and the plecopteran genus *Stenoperla* (Campbell, 1981b). The Megaloptera seems most diverse in the northeast of Australia and has reduced diversity down the eastern coast.

Diptera. The Diptera or two-winged flies is a large order in which only a small proportion of species has aquatic larvae. Dipteran larvae fill a variety of niches in aquatic environments. They range in habits from planktonic to benthic, from carnivorous to detritivorous and xylophagous. They occur in all types of habitats, from large streams and lakes to small rainpools. Overall, the Australian aquatic dipteran fauna does not diverge significantly from that elsewhere and contains all major and most minor families. The most notable absentees are the Deuterophlebiidae (mountain midges) and the Ptychopteridae (mountain craneflies), both of which, however, are quite small families. Knowledge of Australian aquatic dipterans is extremely patchy. Some groups (notably those with pestiferous biting adults, such as the Culicidae and Simuliidae) are well-known, at least taxonomically, while for others we know little beyond the fact that they occur in Australia.

Williams (1981c) distinguishes between those dipteran families where all or most species have aquatic larvae and those where most species are terrestrial. The first category includes Simuliidae, Blephariceridae, Chironomidae, Ceratopogonidae, Culicidae, Dixidae, Ephydriidae, Tanyderidae and Thaumaleidae. Families in which larvae are more often terrestrial than aquatic include the Tipulidae, Psychodidae, Athericidae (=Rhagionidae), Tabanidae, Stratiomyidae, Empididae, Dolichopodidae, Syrphidae and Muscidae.

The larvae of the Simuliidae or blackflies are passive filter-feeders and thus restricted to lotic habitats. They do occur, however, in a variety of flowing waters, from gutters to large rivers. In temporary habitats, they may survive dry periods as drought resistant eggs, although this is yet to be demonstrated (Mackerras & Mackerras, 1948). Adults of some species bite humans and stock and may cause significant problems in northern Queensland. Three simuliid genera occur in Australia: *Austrosimulium*, *Cnephia* and *Simulium*. The first two have Gondwanan affinities, while *Simulium* is a widespread Northern Hemisphere genus thought to have reached Australia via a northern route (Williams, 1981c).

The Blephariceridae or net-winged midges is another family whose larvae are restricted to flowing waters, usually cool, upland streams. The composition of the Australian fauna, its evolution and what is known of its ecology have been reviewed by Zwick (1981a). The Australian fauna is remarkably rich, containing 25 species (cf. only 22 in North America; Merritt & Cummins, 1978) in two subfamilies, the Blepharocerinae (seven species) and the Edwardsininae (18). All species are restricted to the eastern coastal strip of mainland Australia or to Tasmania. Interestingly, although the Edwardsininae is common in Tasmania, with seven species, the Blepharocerinae is absent, even though there appears

to be abundant suitable habitat. The blepharicerids have been cited as a group likely to provide evidence for transantarctic dispersal (Hennig, 1960; Craig, 1969). Zwick (1975; 1977), however, on the basis of detailed studies, suggests that this is unlikely to be the case, believing that the group probably entered by a northern route.

The Chironomidae or midges forms a ubiquitous component of the benthos of inland waters. They are present in lakes, both saline and fresh, streams, wetlands and temporary waters ranging from large lakes to small puddles. Although there have been two substantial taxonomic works on the group in Australia (Freeman, 1961; Brundin, 1966), the fauna is so large and diverse that it must be considered poorly known taxonomically, particularly the larvae. Even so, the Australian chironomid fauna, as a whole, does not appear unusual by comparison with other regions. All major subfamilies occur (Williams, 1980a; Edward, 1986) and most described species either are typical members of well-known cosmopolitan genera (including *Chironomus*, *Tanytarsus*, *Procladius*, *Cricotopus*, *Corynoneura*, *Polypedilum* and *Stenochironomus*) or are species also present in other zoogeographical regions (Freeman, 1961). There are, however, two smaller and more interesting elements in the fauna. The first is a peculiarly Australian element of nine genera (16 species) known only from Australia and New Zealand (Freeman, 1961). The second is a group with an apparently transantarctic distribution. This group, which mainly includes species distributed in the cool upland streams of southeastern Australia, is discussed in detail by Brundin (1966) and includes the Podonominae, Aphroteniinae and Paraheptagyia. With regard to the more widely spread chironomids, the subfamilies Orthocladiinae and Tanypodinae tend to be more abundant in the southeast, while the Chironominae is more common in warmer areas (Colless & McAlpine, 1970).

The Ceratopogonidae or biting midges is a small family represented by about 200 Australian species in 29 genera of which four are dominant: *Culicoides*, *Dasyhelea*, *Forcipomyia* and *Atrichopogon*. Fifteen of the Australian genera have worldwide distributions. Only one, *Astroconops*, appears to be endemic (Colless & McAlpine, 1970). Ceratopogonid larvae survive in a wide variety of aquatic habitats, including streams and lakes as well as marine intertidal and inland saline waters.

The Culicidae is taken here to include two subfamilies: the Culicinae or mosquitoes and the Chaoborinae or phantom midges (following Colless & McAlpine, 1970). The Culicinae is undoubtedly the best-studied aquatic dipteran family in Australia because of the significance of mosquitoes as pests and potential disease vectors for both humans and domestic animals. Petr (1981) reviews the literature on mosquito-borne disease in relation to Australia. Mosquito larvae live in all types of inland waters, as well as brackish, tidal pools. They are particularly rapid colonizers of very small, temporary water-bodies and, partly as a result, are widespread throughout Australia. The culicine fauna consists mostly of Culicini and seems largely derived from a northern tropical fauna although two anopheline genera also occur. It includes several widespread species such as *Culex fatigans* and *Aedes aegypti*. There are no endemic genera, but several subgenera are endemic (Colless & McAlpine, 1970). Only four genera (eight species) of the Chaoborinae occur. They have not been studied well, despite the fact that their planktonic larvae may sometimes cause problems in water supply reservoirs.

The other four dipteran families with larvae confined to aquatic habitats are small, relatively poorly known and not considered here.

For most of the dipteran families in which only some larvae are aquatic, relatively little is known about the aquatic species. Nevertheless, some of these may play important ecolog-

Table 7.15 The families of Coleoptera occurring in Australia which are mainly or entirely aquatic, or which have only a few aquatic species. (After Williams, 1980a; 1981c)

MOSTLY AQUATIC	FEW AQUATIC SPECIES
Gyrinidae	Curculionidae
Dytiscidae	Chrysomelidae
Hydraenidae	Staphylinidae
Helodidae	Georyssidae
Helminthidae	Limnichidae
Hydrochidae	Ptilodactylidae
Hydrophilidae	Heteroceridae
Halophilidae	Carabidae
Hygrotidae	
Noteridae	
Psephenidae	
Spercheidae	
Sphaeriidae	

cal roles in aquatic ecosystems. For example, tipulid larvae appear to be important in breaking down wood in New Zealand streams (Anderson, 1982) and may play a similar role in Australia. It would appear that aquatic Australian representatives of these families belong to widespread genera.

Coleoptera. The Coleoptera or beetles is one of two orders in which both larvae and/or mature forms may be aquatic; the other order is the Hemiptera. The beetles constitute the largest order of insects, but only a small proportion of the order is aquatic. Thirteen coleopteran families in Australia are entirely or mainly aquatic, while a further eight have a few aquatic representatives or have species which occur in submarginal, semi-aquatic habitats (Table 7.15).

The Australian fauna seems generally unremarkable, with a low level of endemism above the species level. Two families are known in sufficient detail for further comment: the Dytiscidae and Psephenidae. The Australian Dytiscidae has been revised by Watts (1978), who recognizes 174 species in 36 genera. Two further species have been described by Zwick (1979b; 1981b). The Bassian Region, including the southwest of Western Australia and southeastern Australia with Tasmania, has the most diverse fauna. Many genera and species are restricted to this region (Watts, 1978). The northern, Torresian Region is the next most diverse and shares a number of species with New Guinea. The gap between these two faunas has been identified by Watts (1978) as lying between 20 to 22°S, which overlaps the 19 to 21°S zone of disjunction which Watson & Theischinger (1984) note for odonatans, plecopterans and megalopterans.

The Australian Psephenidae or water pennies has been revised by Davis (1986). With the exception of one species, Australian larvae are restricted to flowing waters, while adults are terrestrial. Davis (1986) recognizes 18 species, all in *Sclerocyphon*. This genus at present is restricted to Australia, although there is a larva described from Chile which is either congeneric or belongs to a closely related genus (Davis, 1986). Most species of *Sclerocyphon* are restricted to streams near the east coast of mainland Australia or Tasmania, with the greatest diversity in the southeast. One species, *Sclerocyphon fusca*, has been recorded from Stokes Creek, Northern Territory. All eight species recorded from Tasmania are endemic in that island. The Tasmanian fauna also includes the sole lacustrine species (Davis, 1986).

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Hemiptera. Like the Coleoptera, the Hemiptera or bugs is a large insect order with only a relatively small proportion of aquatic species. Most aquatic hemipterans have both larvae and adults aquatic and, unlike the terrestrial hemipterans which are overwhelmingly phytophagous, aquatic species are mostly carnivorous. Lansbury (1981), in a recent review of the Australian aquatic Hemiptera, notes a high level of species endemism (80%) and a lower generic one (17.5%).

In general, the Australian hemipteran fauna is not particularly distinctive. Fourteen families occur in Australian inland waters and two more in adjacent marine waters (Table 7.16) (Lansbury, 1981). All of these also occur elsewhere and no major families appear absent. More species seem to be present in the north, particularly the northeast, than in southern Australia and Lansbury (1981) suggests that the Australian fauna is derived largely from the Oriental Region.

Other Orders. Several other insect orders have aquatic representatives in Australia. The Mecoptera, or scorpionflies, has a single family, the Nannochoristidae, with aquatic larvae. The family has a transantarctic distribution. A single genus, *Nannochorista*, occurs in southeastern mainland Australia and Tasmania. The three Australian species are endemic, but the genus also occurs in South America.

Three families of Neuroptera or lacewings are known to have aquatic or semi-aquatic larvae. All three have been recorded from Australia, though little else is known about them. Aquatic larvae of the nymphaline Pyralidae (Lepidoptera) are widespread, especially in northern Australia, but rarely abundant (Common, 1970). A single species of aquatic wasp (*Austromicron zygopterorum*, Hymenoptera : Trichogrammatidae) has been described from Australia by Tillyard (1926), but nothing more is known of it.

Fishes

All four of the classes into which fish are grouped are found in Australian inland waters, though it is, as elsewhere, the Actinopterygii which includes most species. A systematic summary of the fish fauna is given in Table 7.17. This table, it may be stressed, is somewhat arbitrary for it is not easy to decide exactly what species should be counted: many species of fish migrate between inland and marine waters as a normal part of their life cycle and others are essentially marine species which occur in inland waters as vagrants.

Table 7.16 Composition of the hemipteran fauna of Australian inland waters. (After Lansbury, 1981)

FAMILY	NUMBER OF GENERA	NUMBER OF SPECIES
Saldidae	1	7
Ochteridae	2	3
Gelastocoridae	1	20
Mesovelidae	1	2
Veliidae	2	9
Gerridae	4	9
Hebridae	2	2
Hydrometridae	1	6
Naucoridae	2	4
Belostomatidae	2	4
Nepidae	5	9
Pleidae	1	2
Notonectidae	5	32
Corixidae	5	29

Several points emerge from the table that justify comment. First, the total number of species present is small relative to the number present on other continents. Less than 200 species can be regarded unequivocally as inland species. Second, endemicity is high. And third, several families characteristic of fresh waters outside Australia either are absent or have been introduced by man. Of special note in this regard are the families Salmonidae, Cichlidae and Cyprinidae.

Despite the lack of diversity within the native fish fauna, many elements are of considerable interest to ichthyologists. Perhaps of greatest interest are the Galaxiidae (southern trout) and *Neoceratodus forsteri*. The Galaxiidae is a family confined to the Southern Hemisphere, but which is most abundant and diverse in Australia. *Neoceratodus forsteri* is the only choanichthiid in Australia and has persisted relatively unchanged for some 150 million years (Fig. 7.9a).

The greatest diversity of native fishes occurs in the northeast, where some 50 to 59 species have been recorded. Rather lower diversity (40 to 49) occurs in the northwest and southeast. The Murray-Darling Basin and Tasmania have less than 30 species each. Central and most of Western Australia have less than 20 each. As a general rule, graylings, smelts, galaxiids and blackfish are important in southern temperate regions. Northern tropical regions are dominated by other groups (e.g. Scleropagidae, Tetrapontidae, Melanotaenidae, Centropomidae). Galaxiids are important in Tasmania and Percichthyidae in the Murray-Darling Basin. The southwest has galaxiids and gobies (Gobiidae) as important elements. Permanent freshwater lakes, streams and rivers are clearly the most suitable habitats for fish, but species also occur in saline lakes, underground waters and some temporary lakes and streams.

The extent of thorough systematic studies is much less than might be suggested by the number of illustrated books now available on Australian freshwater fishes. Even so, Australian ichthyology is served well by the texts of Lake (1971; 1978), McDowall (1980), Allen (1982), Cadwallader & Backhouse (1983) and Merrick & Schmida (1984). The review papers of Pollard *et al.* (1980) and McDowall (1981) are also useful sources of information.

Amphibians

The only amphibian order found in Australia is the Anura (frogs). The extent of the association between frogs and inland waters varies from one that is intimate, when both adults and juveniles can be regarded as fully aquatic, to one that is slight at best, with neither adults nor juveniles needing significant access to free water. Nevertheless, most frogs are associated with inland waters either as amphibious adults or aquatic juveniles and it is simpler to discuss the group as a whole, than to attempt an artificial split between those that are aquatic and those few that are not.

The higher systematics of frogs is a subject of lively debate, but for present purposes it suffices to recognize the occurrence of five families: Hylidae, Myobatrachidae, Microhylidae, Ranidae and Bufonidae. The last family involves a single, introduced species, *Bufo marinus*. An overview of the systematics of Australian frogs is given in Table 7.18. As the table indicates, the frog fauna of Australia is diverse, particularly the families Hylidae and Myobatrachidae. Endemicity is extremely high, with just a few species shared with adjacent land areas. Diversity is highest in northern tropical regions. The sorts of water-bodies utilized by frogs are many and varied. All types except saline lakes seem to contain adults or larvae at one time or another. Temporary pools, water in tree stumps, permanent lakes, rapid streams and slowly flowing water all have characteristic species. In arid regions, frogs make use of temporary waters for breeding and adults are

Table 7.17 Composition of fish fauna of Australian inland waters. (After Williams, 1983a); ¹ number of endemic genera or species shown in parentheses; ² one introduced; ³ all introduced.

FAMILY	COMMON NAME	NUMBER OF GENERA ¹	NUMBER OF SPECIES ¹
Class: Cyclostomata			
Geotriidae	lampreys	1	1
Mordaciidae	lampreys	1	2(2)
Class: Chondrichthyes			
Pristiidae	sawfishes	1	1
Class: Choanichthyes			
Ceratodontidae	lung-fishes	1(1)	1(1)
Class: Actinopterygii			
Anguillidae	eels	1	4(1)
Clupeidae	herrings	2(1)	3(1)
Scleropagidae	barramundi	1	2(1)
Retropinnidae	smelts	1	2(2)
Lepidogalaxiidae	scaled galaxias	1(1)	1(1)
Galaxiidae	southern trout	3(2)	20(18)
Prototroctidae	southern grayling	1	1(1)
Aplochitonidae	whitebait	1(1)	1(1)
Ariidae	fork tail catfishes	1	2(1)
Plotosidae	eel tail catfishes	4(2)	11(8)
Belontidae	needle fishes	1	1(1)
Melanotaeniidae	rainbow fishes	3(1)	13(11)
Atherinidae	silversides, hardyheads	3(2)	11(10)
Synbranchidae	one-gilled eels	2 ²	3 ² (2)
Scorpaenidae	scorpion fishes	1(1)	1(1)
Centropomidae	glass fishes, silver barramundi	1	1
Ambassidae	chanda perches, etc.	2(1)	7(4)
Percichthyidae	Australian basses, cods	3(3)	7(7)
Teraponidae	terapon perches, grunter	8(3)	20(16)
Kuhliidae	flagtails, mountain perches	3(2)	6(5)
Electridae	gudgeons	15(4)	33(19)
Gobiidae	gobies	8(3)	15(8)
Kurtidae	nursery fishes	1	1
Soleidae	soles	2	3(2)
Gadopsidae	blackfish	1(1)	1(1)
Apogonidae	cardinal fishes	1	1
Toxotidae	archer fishes	1	1(1)
Mugilidae	mullet	1	1(1)
Bovichtyidae	tupong, congolli	1(1)	1(1)
Salmonidae ³	salmon, trout	3	5
Poeciliidae ³	mosquito fish, guppies, etc.	4	7
Amphipnoidae ³	cuchia	1	1
Percidae ³	redfin	1	1
Cyprinidae ³	carps, tench, etc.	5	6
Cichlidae ³	cichlids	3	4

essentially terrestrial. The species, *Cyclorana platycephala*, the "water-holding" frog, breeds in temporary pools, creeks or claypans. When such ephemeral waters dry, this unique frog burrows into soil and makes a cocoon-like impervious chamber filled with water. Here it spends the long, dry periods characteristic of its environment.

A key reference to the systematics of the frog fauna is the catalogue of Cogger *et al.* (1983). The texts of Barker & Grigg (1977), Cogger (1986) and Tyler (1982) are also valuable in a more general way.

Reptiles

A variety of reptiles is associated with aquatic situations in Australia: tortoises, crocodiles, lizards and snakes. A summary of the composition of the aquatic reptile fauna is given in Table 7.19. The numbers of species given in this table are approximate since the division between species that can be regarded as aquatic and those that are essentially terrestrial, but often found near water, is not easily determined. This is

particularly so in the case of lizards and snakes – within which groups there are, of course, many entirely terrestrial species. A group of specialized aquatic snakes from the sub-family Homalopsinae, found in northern rivers, estuaries and coastal mangrove flats, feeds on crabs, fishes and other aquatic vertebrates. Another group, the file snakes of the family Acrochordidae, contains two species found in northern rivers and estuaries and which eat fishes and crabs. All the Chelidae (freshwater tortoises) are pleurodirous (head and neck fold horizontally) and the family is confined to Australia, New Guinea and South America. In contrast, the sole representative of the Carettochelydidae, *Carettochelys insculpta*, is cryptodirous (the head and neck fold vertically). This strange inhabitant of several rivers in the north of the Northern Territory has paddle-shaped limbs like those of a marine turtle.

Reptilian diversity is greatest in northern Australia. This is not surprising given the physiological need of reptiles for relatively high ambient temperatures. Nevertheless, there are many species in southern regions, particularly chelids and lizards. Permanent fresh waters, often associated with large

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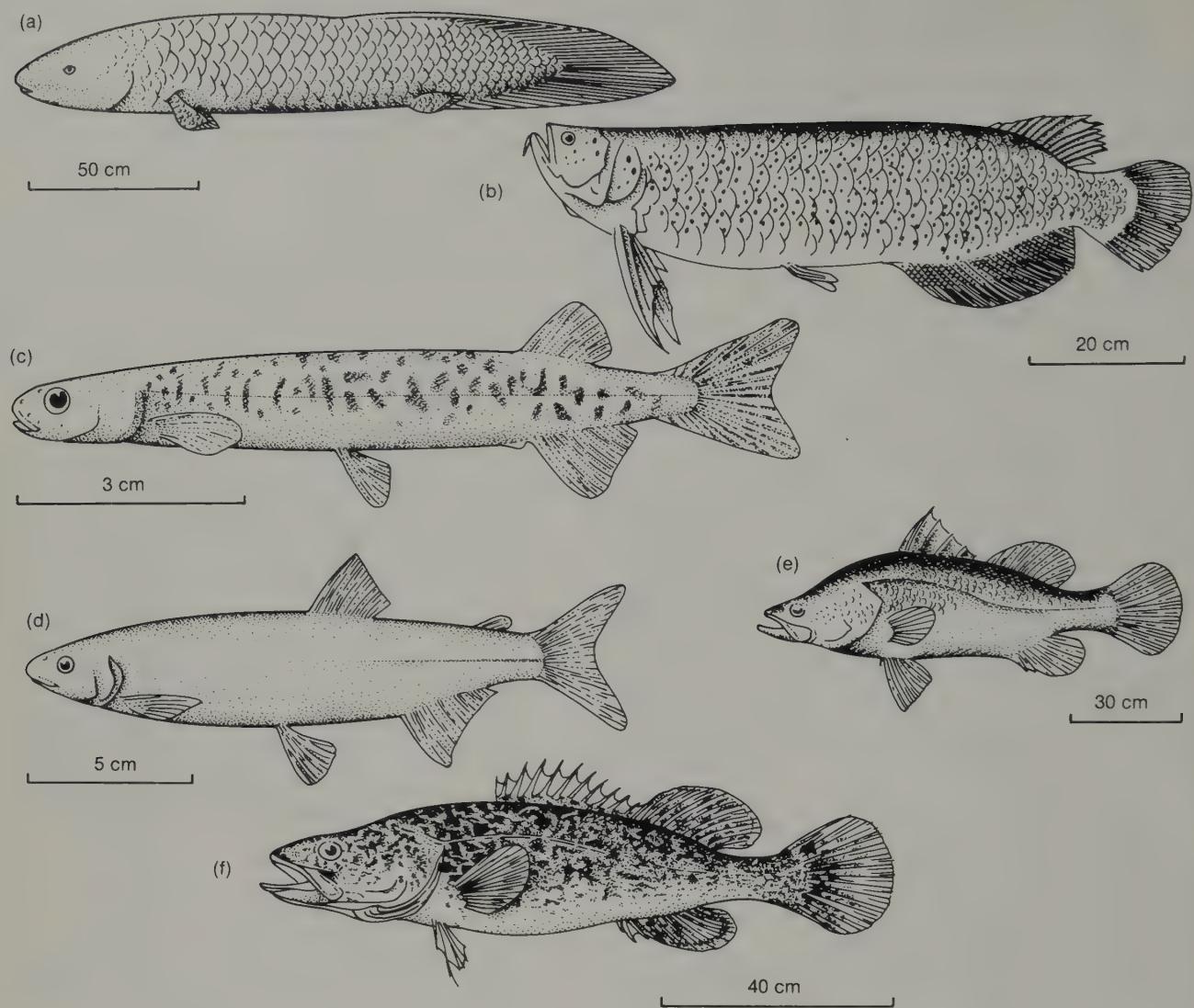


Figure 7.9 Some significant fish of Australian inland waters. (a) lungfish; (b) spotted barramundi; (c) common galaxias; (d) Australian grayling; (e) silver barramundi; (f) Murray cod. (After Williams, 1983a)

[R. Evans]

rivers, are preferred habitats. No reptiles actually live in salt lakes when they are filled, though one crocodile, *Crocodylus porosus*, is found in marine water and estuaries as well as in fresh water in northern Australia which it shares with another species, *C. johnstoni*, an exclusively freshwater inhabitant.

Cogger (1986) and Cogger *et al.* (1983) are again valuable sources of information on this group of aquatic vertebrates.

Birds

Ten bird orders include species characteristically found near or on inland surface waters which they use for feeding, breeding, resting or as refugia. The number of species and families involved is indicated in Table 7.20. Again, difficulty was experienced in deciding which species to count in the table, for the separation between birds of the coast, land and inland waters was often subjective. The table, nevertheless, will provide a useful working idea of the extent of diversity and the sorts of species present. The Order Passeriformes provided the greatest difficulty in this regard. It should be noted that the species of passerines included in the table are *Acrocephalus stentoreus*, *Epthianura crocea*, *Megalurus*

gramineus and *Malurus coronatus*. These species live amongst emergent reeds or, in the case of *M. coronatus*, bushes and trees fringing certain northern rivers. Including the passerines, over 100 species of birds associate with Australian inland waters. Many of them are endemic, but because marine barriers can be traversed more easily by birds, endemicity is not as great as in the amphibians and reptiles.

The great mobility of birds also means that patterns of geographical distribution are broader for them than for most other aquatic animal groups. Notwithstanding, a few general patterns can be recognized. There is a large northern region characterized by species whose life cycles correlate closely with the flood-drought regime of most rivers there. Several species of waterfowl are restricted to or breed only in this region. The pygmy geese (*Nettapus* spp.) and the whistle ducks (*Dendrocygna* spp.) provide examples. There is a central, arid region where nomadism is an important waterbird adaptation. The Murray-Darling Basin is a third region. Here, the large number of billabongs and wetlands associated with the major rivers provides extensive habitat for many birds, particularly waterfowl. Finally, the temperate, wetter areas of the southwest and southeast constitute a fourth

region. Amongst waterfowl characteristic of this region, *Cygnus atratus*, *Tadorna tadornoides* and *Cereopsis novaehollandiae* are notable.

All surface waters have attracted the attention of birds, either as a source of food, a place to rest or hide or as a breeding habitat. Six habitats are of particular significance: flooded areas in woodland, irrigated pastures, wetlands (*i.e.* meadow swamps and natural wet pasture), reedswamp, open fresh water and salt lakes. The principal types of waterbird which use these habitats, and to what end, are shown in Table 7.21.

Australian bird life, aquatic or otherwise, has attracted attention from both amateur and professional ornithologists. There is no shortage, therefore, of books to identify species and from which to obtain general information on waterbird habits and distribution. Slater (1970) and the *Reader's Digest Complete Book of Australian Birds* (1986) may be mentioned in this regard. For detailed information on geographical distribution, the *Atlas of Australian Birds* (Blakers *et al.*, 1984) is an outstanding reference.

Information on bird ecology is less easily available, not least because the amount known is less, but Frith's (1977) text on waterfowl provides an introduction to this important group of waterbirds.

Mammals

The Platypus, a few species of murid rodents and the introduced Water Buffalo are the only mammals which inhabit Australian fresh waters. Marsupials, which are the dominant mammalian fauna, are not aquatic in Australia. This is not the case in South America where an aquatic marsupial frequents inland waters. By far the most interesting of the aquatic mammals is *Ornithorhynchus anatinus*, the Platypus, an animal which combines a unique mixture of mammalian, reptilian and individual features. There is no question, however, of its position as a mammal. It is so distinctive that it is placed – together with another curious Australian mammal, *Tachyglossus aculeatus* – in a distinct subclass, the Prototheria. The natural distribution of the platypus is eastern Australia, where it occurs widely in Tasmania and in most of the large rivers east and west of the Great Dividing Range. It also is found in isolated parts of South Australia, but is absent from Western Australia and from central regions. Large permanent freshwater lakes and rivers are its natural environment, but it now occurs in several man-made impoundments.

Two murid rodent species can be regarded as part of the aquatic fauna of Australia. *Hydromys chrysogaster*, the Water Rat, is distributed widely throughout Australia in more or less permanent fresh waters. *Xeromys myoides*, the False Water Rat, is found in waters not far from the coast in the Northern Territory and eastern Queensland. Additionally, a few other murids are usually or often found associated with swamps, lakes and rivers and, whilst they may possess no obvious morphological adaptations to an aquatic life-style, they perhaps should be regarded as part of the aquatic vertebrate fauna. Notably, they are *Rattus lutreolus*, *R. colletti*, *Mastacomys fuscus*, *R. tunneyi* and *R. fuscipes*. All rodents found in Australian waters belong to the family Muridae.

The Water Buffalo (*Bubalus bubalis*) was introduced in the early part of the 19th Century. It is confined to the northern coastal plain of the Northern Territory where it is always found near billabongs and rivers. Feral pigs, *Sus scrofa*, although not truly aquatic, are often found wallowing and feeding in inland swamps, rivers and billabongs.

Table 7.18 Composition of Australian frog fauna. (After Cogger *et al.*, 1983), ¹ most diverse genera are *Litoria*, *Ranidella* (= *Crinia*), *Cyclorana*, *Limnodynastes*, *Uperoleia*, ² introduced (see text).

FAMILY	NUMBER OF GENERA	NUMBER OF SPECIES
Myobatrachidae ¹	20	98
Hylidae	3	71
Microhylidae	2	8
Ranidae	1	1
Bufonidae ²	1	1

Some important and comprehensive references to Australian aquatic mammals are those by Ride (1970), Griffiths (1978), Watts & Aslin (1981) and Grant (1984).

DISTINCTIVE FEATURES OF THE FAUNA OF INLAND WATERS

Throughout the preceding discussions, much has been made of distinctive features concerning individual groups. It is appropriate to conclude this Chapter by reviewing briefly the general nature of these features and to consider the fauna as a whole.

One of the most distinctive features is the high level of endemism. Species endemism is high in all groups except the Protozoa, Nematoda and Polyzoa and in some groups is almost complete (e.g. in many crustacean and insect orders). Generic endemism, likewise, is high in many groups and almost complete in a few. Important in this respect are the Isopoda, Amphipoda, Plecoptera, Odonata and Arachnida amongst the arthropods and the Temnocephaloidea, Turbellaria, Mollusca and Amphibia amongst non-arthropods. While endemism is not so high at the familial level, there are several families of aquatic animals found only in Australia. Invertebrate endemic families are the Anaspidae, Koonun-

Table 7.19 Composition of Australian reptile fauna associated with inland waters. (After Cogger *et al.*, 1983; Williams, 1983a)

FAMILY	NUMBER OF GENERA	NUMBER OF SPECIES
Lizards		
Agamidae	2	2
Varanidae	1	5
Scincidae	1	3
Snakes		
Boidae	1	1
Acrochordidae	1	2
Colubridae	5	5
Elapidae	5	5
Crocodiles		
Crocodylidae	1	2
Tortoises (turtles)		
Chelidae	5	15
Carettochelydidae	1	1

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Table 7.20 Birds characteristically associated with Australian inland waters. (After Williams, 1983a)

ORDER	FAMILY	COMMON NAME	NUMBER OF GENERA	NUMBER OF SPECIES
Podicipediformes	Podicipedidae	grebes	3	3
Pelecaniformes	Pelecanidae	pelicans	1	1
	Anhingidae	darters	1	1
	Phalacrocoracidae	cormorants	1	4
Ciconiformes	Ardeidae	herons, egrets, bitterns	5	13
	Ciconiidae	storks	1	1
	Threskiornithidae	ibises, spoonbills	3	5
Anseriformes	Anatidae	ducks, geese, swans	13	19
Falconiformes	Accipitridae	eagles, harriers	2	2
Galliformes	Pandionidae	ospreys	1	1
Gruiformes	Phasianidae	quail	1	1
	Gruidae	cranes	1	2
Charadriiformes	Rallidae	rails, crakes, hens, coot	7	13
	Jacanidae	jacanas	1	1
	Rostratulidae	painted snipe	1	1
	Charadriidae	plovers, dotterels	3	7
	Scolopacidae	curlews, snipe, sandpipers, stints	8	17
	Recurvirostridae	avocets, stilts	3	3
	Laridae	gulls, terns	5	9
Coraciiformes	Alcedinidae	kingfishers	2	2
Passeriformes	Sylviidae	warblers	2	2
	Maluridae	wrens	1	1
	Ephthianuridae	chats	1	1

gidae and Psammaspididae (all syncarids), the odonate Lestoideidae and Hemiphlebioidae, the trichopteran Plecotarsidae and the cnidarian Australomedusidae. Endemic vertebrate families include the Gadopsidae and Lepidogalaxiidae (fishes) and the Ornithorhynchidae (Platypus).

Another distinctive feature is the increased importance of particular groups or families *vis-a-vis* their importance in waters on other continents. Taxa of interest in this respect can be divided into those essentially cosmopolitan, or at least found in some waters of the Northern Hemisphere, and those almost confined to waters of the Southern Hemisphere. The former group includes temnocephalids and the families Dugesiidae (Turbellaria), Centropagidae (Copepoda), Leptophlebiidae (Ephemeroptera) and in the Trichoptera the Hydrobiosidae, Hydroptilidae and Leptoceridae. All are much more diverse in Australian inland waters than in waters elsewhere. The latter, southern group includes especially the Hyriidae (freshwater mussels), Parastacidae (Decapoda), Phreatoicidea (Isopoda), Galaxiidae (Pisces) and the Myobatrachidae (Amphibia). Allied to this group are several other families which have not radiated widely in Australia, but which, nevertheless, display distributions confined to other southern land-masses. The Nannochoeristidae and all four families of the Plecoptera provide examples.

A third distinctive feature is the natural absence or only slight occurrence in Australia of several aquatic groups which are characteristically common in many inland waters elsewhere. Notable examples are the mayfly families Heptageniidae and Ephemerellidae, the trichopteran Limnephilidae, the isopodan Asellidae, the cladoceran Holopedidae, Leptodoridae, Polyphemidae and Cercopagidae, the fish Salmonidae, Cyprinidae and Cichlidae, the amphibian Ranidae and, for birds, the Phoenicopteridae (flamingos) and Gaviiformes (loons). Excluding recent introductions, all of these have few or no representatives in Australia (although flamingos are known as fossils). Interestingly, there is no extant aquatic Australian marsupial, although an aquatic

South American marsupial does exist. Except for those murids noted above, eutherian non-marine aquatic forms are absent.

In addition to these general features, and features which apply to individual groups, there are many species within the Australian aquatic fauna that are distinctive in their own right. Only a few examples are needed to illustrate the point. *Coxiella striata*, a gastropod, is probably the most salt tolerant of all molluscs known and lives in salt lakes throughout the southern part of Australia. *Haloniscus searlei*, an isopod, is another inhabitant of salt lakes and appears to be the only oniscid found in such habitats. *Anaspides tasmaniae*, the Tasmanian Mountain Shrimp, is morphologically close to the presumed ancestor of all modern malacostracans. The two frogs of the genus *Rheobatrachus* have a unique method of brooding their young: they incubate them in their stomachs. *Neoceratodus forsteri*, the Queensland Lungfish, is one of only three choanichthyid fish still extant. And last but not least, *Ornithorhynchus anatinus* is considered so different from all other mammals that it is placed (with, as indicated, the Tachyglossidae) in a separate mammalian subclass, the Prototheria.

Finally, it may briefly be noted, certain aquatic habitats in Australia maintain a unique faunal combination. This applies above all to salt lakes. Thus, in Australian salt lakes, *Artemia* and ephydriids, two sorts of animal often present in salt lakes on other continents, are usually not present. Instead, the fauna usually comprises *Parartemia* (an endemic genus of brine shrimp), *Daphniopsis* (a cladoceran), *Calamoecia* (a calanoid copepod) and several species of ostracods.

In response to the special nature and history of the Australian aquatic environment, a fauna has developed unlike that on any other continent. This fauna constitutes a veritable Aladdin's cave for modern biologists and a unique store of genetic diversity for posterity.

Table 7.21 Some major types of waterbird habitat and the principal sorts of waterbirds using them. (After Williams, 1983a)

FLOODPLAIN FOREST	IRRIGATED PASTURE	MEADOW SWAMPS NATURAL WET PASTURE	REEDSWAMP	OPEN WATER	SALT LAKES
Dominant vegetation: trees, grass, sedges, rushes	grass, semi-aquatic macrophytes	sedges, rushes	rushes, sedges, reeds	submerged hydrophytes	none
Feeding area for: ibises, snipe, dotterels, kingfishers	mountain ducks, ibises, herons	spoonbills, egrets, herons, waterhens, brolgas, stilts, ducks, swans, yellow chats	spoonbills, egrets, swans, coots, ducks, red warblers, bitterns, crakes, rails, little grassbirds, yellow chats	swans, musk ducks, cormorants pelicans, darters, hawks, waterhens	banded stilts, avocets, red-capped dotterels, red-necked stints, curlew, sandpipers
Breeding area for: ducks, cormorants, kingfishers	plovers, dotterels	ducks, crakes, rails, little grassbirds, yellow chats	cormorants, ibises, swans, grebes, bitterns, red warblers, jacanas, little grassbirds, crakes, rails, swamp harriers, yellow chats	stilts, avocets	none
Refuge area for: kingfishers, certain ducks	snipe, plovers	little grassbirds, yellow chats	waterhens, ducks, grebes, bitterns, little grassbirds, crakes, rails, red warblers, yellow chats	ducks, swans, grebes, gulls, terns	ducks, swans, gulls, terns,

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8. ORIGINS AND ADAPTATIONS OF THE FAUNA OF INLAND WATERS

W. D. WILLIAMS & G. R. ALLEN

INTRODUCTION

The major features of the Australian inland aquatic environment and the composition and distribution of its fauna are discussed in Chapter 7. A discussion confined to those subjects would be quite incomplete in any text which purports to treat the Australian aquatic fauna comprehensively. There is a clear need to complement it with an account which describes past and present environments against which to view the modern Australian aquatic fauna and its habitats, deals with faunal origins and discusses the adaptations which have evolved in response to the special character of Australian inland aquatic environments. The present Chapter is intended to provide this complementary account. It is, in short, a discussion of the evolution of the Australian inland aquatic fauna (though not a discussion of the nature of evolutionary mechanisms involved).

THE ENVIRONMENTAL SETTING

Many environmental features have been important in the evolution of the aquatic fauna. Among the most obvious are Australia's long geographical isolation, its flat topography and overall aridity. For any adequate understanding of the origins and adaptations of the aquatic fauna, therefore, some knowledge of Australia's geological history, physiography and past climates is essential. All of these matters are discussed elsewhere in this book, but their prerequisitory nature demands at least cursory treatment here.

Geological History

The phenomenon of continental drift has been well documented by palaeomagnetic and other studies (for a review with special reference to Australia see Crook, 1981; Powell *et al.*, 1981). Although opinions differ on details, particularly those on dating, the sequence of events is now generally agreed. For present purposes, tracing only major events will suffice.

The Australian Plate was at first an integral part of the great Pangaean landmass which existed until the early to Middle Triassic and the occurrence of the same higher faunal categories (*viz.* classes, orders, *etc.*) on all continents, including Australia, attests to their common Pangaean ancestry. By the Early Jurassic, however, or by the time that mammals began to evolve, rifting between the northern (Laurasia) supercontinent and the southern one (Gondwana) was almost complete. The two supercontinents remained attached only in the region of what is now the Mediterranean Sea and were elsewhere separated by the Tethys Sea.

Of major importance in the shaping of the contemporary aquatic biota was the subsequent fragmentation of Gondwana during the Cretaceous and early to middle Tertiary. South America began moving away from the African Plate about 125 mybp with final separation occurring about 80 mybp. India and Madagascar, which had been conterminous, also

broke from the African Plate at about 125 mybp; they subsequently diverged from each other about 80 to 90 mybp. The eastern Gondwana landmass, comprising Australia, Antarctica and connecting to South America, appears to have persisted intact for much longer. One result is that several modern vertebrate families and higher taxa have representatives in both South America and Australia. Although there is lack of agreement on the exact time of separation of Antarctica from South America, it appears to have been about 30 to 50 mybp.

Also important in shaping the eventual nature of the Australian aquatic biota was the separation of Australia and Antarctica. This began in the Eocene, about 53 mybp. Even so, and although the continental margins themselves were separate by about 49 mybp, Antarctica and Australia probably remained connected via Tasmania and the South Tasman Rise until as late as the close of the Eocene, or about 38 mybp. New Zealand has been isolated from Australia for a much longer period; it separated from Antarctica about 80 mybp with the formation of the Tasman Sea and the New Caledonian Trough (Crook, 1981).

The high percentage of endemism in the Australian fauna, particularly at generic and specific levels, is a direct consequence of this long period of geographical isolation.

After separation from Antarctica, there was a gradual northward movement of the Australian Plate to its present position. In the middle Paleocene, however, the Australian landmass was situated mainly between latitudes 40° and 70°S (its present position is between 10° and 40°S). The Australian Plate eventually collided with the Sunda Arc in the Late Miocene, about 10 mybp. This proximity to southeastern Asia facilitated colonization, particularly into northern Australia, of many elements of the aquatic fauna of southeastern Asia.

Colonization was promoted by the presence of New Guinea which was connected to Australia by the Torres landbridge as recently as 6,000 to 8,000 years ago. What is now southern New Guinea formed the leading edge of the Australian Plate during its northern migration. The collision of the plate and its accretion with an island arc on the edge of the Pacific Plate gave rise to the final form of our most immediate neighbour. Emergent land, however, did not appear until the end of the Eocene and New Guinea remained an island until a land connection with Australia formed during the Miocene (Loeffler, 1977; Dow, 1977). Thus, New Guinea has served as a stepping stone for a migration of aquatic fauna into Australia for only a relatively short geological period; it has had, nevertheless, a profound influence in shaping the biota of the high rainfall areas of northern and eastern Australia.

In summary, then, the major geological events that most influenced the evolution of the aquatic fauna in Australia are: the break-up of Gondwana, the eventual separation of the Australian Plate and Antarctica, the northward movement of Australia and the collision of the Australian and Pacific Plates.

Physiography

Australia is composed of an ancient orogenic foundation of low-lying strata. This foundation has undergone extensive weathering, and been modified by moderate uplifting along mainly its eastern margin as a result of collision with the Pacific Plate. The most remarkable topographical feature is the wide extent of flat land; 99% of the continent lies below 1,000 m and mean continental elevation is the lowest of any continent. Nix (1981) summarizes the geological evolution of Australia (and New Guinea) and the present account is based mainly on his summary.

Essentially, the tectonic development of Australia involved five major episodes of orogenic activity spanning more than 3,000 million years. Development began with the formation of an Archaean nucleus in Western Australia between 3,000 and 2,200 mybp. Succeeding orogenic provinces formed mainly between 2,200 and 1,900 mybp. These episodes were separated by lengthy periods of platform cover development consisting of sedimentary materials. The Australian continental shield was more or less complete by about 1,200 mybp and stable conditions then prevailed for another 550 million years.

The extensive Trans-Australian Platform Cover began its development about 300 mybp, reaching a maximum during the Cretaceous when extensive seas covered large areas of the plate. This deposition has continued to the present in pericontinental basins and the lowlands of southern New Guinea. The folded rocks characteristic of the East Australian Orogenic Province were deformed by an episode of tectonic events from the Cambrian to the Late Triassic, events some 500 to 200 mybp.

During the northward drift of Australia after separation from Antarctica, there was increasing interaction with the Pacific Oceanic Plate. This led to a shift of orogenic activity to the north and east. The activity was characterized by upwarping and associated flood basalts which gave rise to the present Eastern Highlands. Only moderately high elevations were produced, however, and relief in the late Cainozoic was not much greater than today. According to Wellman (1974), the last uplifting was post-Oligocene and less than 300 metres. Drainage systems and general topography at that time were similar to those of the present.

Localized vulcanism, commencing in the Mesozoic, occurred in the Eastern Highlands from near Cooktown in northern Queensland to the Grampians in Victoria. It continued throughout the Tertiary (Wellman & McDougall, 1974) and ceased only recently, with the last basaltic flows occurring in north Queensland and western Victoria some one to two thousand years ago. Vulcanism continues to play a major role in shaping the present landscape of New Guinea.

The central lowlands, which cover most of the arid interior of Australia, are composed of two large sedimentary basins, the Murray-Darling and the Gulf of Carpentaria. Associated with them are several smaller basins. All are characterized by low relief and gentle gradients. The internally drained Lake Eyre basin was formed by a small downwarp in the late Tertiary. Much of the continental interior contains relatively stable systems of longitudinal sand dunes and sheets; these represent the largest edaphic entity of the continent and have existed for at least 300,000 years (Bowler, 1976). The most recent period of widespread dune evolution occurred at the same time as the last glaciation (Bowler & Polach, 1971).

More than half of the Australian coastline is fringed with well-developed dunes and sand ridges. Often, these form local basins of variable size containing permanent fresh or saline water. Most of these dunes are of relatively recent origin, but some were formed in the early or middle Pleistocene.

Finally, it may be noted, New Guinea is mainly excluded from the present discussion, although it is intimately related geologically, as well as biologically, to the Australian continent. It represents the youngest of the five major orogenic provinces on the Australian Plate.

Past Climates

Information on past climates is generally sparse and localized. It is based primarily upon evidence from fossil pollen, lake sediments and marine deposits. Much more about this subject needs to be known because, as Galloway & Kemp (1981) among many others stress, climate is the key environmental factor in biogeography. Thus, the present distribution of the Australian aquatic fauna can only be interpreted in the light of past climatological as well as geological events. Climatic events of the Quaternary are of particular importance in this regard, but short-term climatic oscillations should not be ignored. The latter may be measured in only tens of years, but can bring about significant expansion or contraction of distributional ranges of populations.

During most of the Paleocene, Australia and Antarctica were linked and located in high southern latitudes. Evidence from deep-sea carbonate oozes indicates that sea temperatures then surrounding Australia were considerably warmer than at present. Oxygen isotope ratios, for example, suggest that mean annual sea-surface temperatures on the Campbell Plateau were about 18 to 20°C. Antarctica was apparently free of ice at that time. Scattered samples of fossil pollen (mainly from the southeast and coastal Queensland) suggest that the climate, at least in eastern Australia, was cool to temperate with relatively high amounts of rainfall.

What is known about Tertiary climates has been summarized by Kemp (1981). During the Eocene, sea temperatures warmer than those at present continued to prevail and would have greatly affected inland climates since major marine transgressions occurred across much of southern Australia. By the end of this epoch, however, sea-surface temperatures had gradually declined to about 10°C on the Campbell Plateau. Palynological evidence indicates that a relatively warm and moist climate then prevailed over much of Australia. The Southern Beech, *Nothofagus*, for example, occurred widely in the inland (Eyre Formation) and rainforest, probably of the closed canopy type, appears to have been widespread.

During the Oligocene, sea temperatures dropped dramatically as indicated by the 6 to 7°C values on the Campbell Plateau. Australia continued its northward migration and the rift with Antarctica became well developed, with the concurrent development of a circum-polar circulation. Although the fossil evidence available for this period is sparse, climatic conditions apparently were drier and cooler than in the Eocene and there was a consequent decrease in floral diversity. Ice probably was well developed on Antarctica during this epoch, although there is little known about its nature and extent.

In the Early Miocene, there appears to have been a warming of Australian seas and an increase in the amount of inland precipitation. Even so, in response to the rapid build-up of an ice sheet on Antarctica, southern climates had cooled considerably by Late Miocene times. During the Middle Miocene, palaeobotanical evidence from central Australia suggests that rainforest cover was replaced, at least periodically, by grasslands. There also are indications of relatively rapid retreats of rainforest in the southeast during the Late Miocene (Kemp, 1981).



Figure 8.1 Major drainage divisions of Australia.

[R. Evans]

From the mid-Miocene to the present, the Australian aquatic biota increasingly has needed to adapt to more arid conditions or needed to migrate in response to aridity. Unfortunately, the chronology of this transition to climatic aridity is not well documented and rates of change no doubt varied greatly according to region. Despite the general continental trend to aridity, however, some areas (*e.g.* the Gippsland Basin of Victoria) appear to have maintained climates which were wetter and warmer than present ones and which persisted until the first Pleistocene glacial period.

The nature of Pliocene and Pleistocene climates has been reviewed by Galloway & Kemp (1981) and the following summary is based on their work. Although climatological data are sketchy, both isotopic sea-surface temperatures and evidence from marine and terrestrial fossils suggest that an initial period with a warm and moist climate during the Early Pliocene (4.3 to 3.9 mybp) was followed by a relatively cool and dry period in the latter part of the epoch. This cool period corresponded to a rapid build-up of ice sheets, particularly in the Northern Hemisphere, which reached about a third to half of their Pleistocene maxima (Shackleton & Kennett, 1975a;b).

Significant events of late Pleistocene and Holocene climates were continued oscillations between cool, dry glacial periods and warmer, moister interglacial periods. During the interglacials, sea temperatures and rainfall were higher than at present. Glaciation on the Australian mainland was minimal and restricted to the Kosciusko Plateau. The last glacial maximum was about 18,000 years ago when temperatures were perhaps 5 to 10°C lower than at present and rainfall in the southeast was about 50% less than at present (De Deckker, 1986). Glaciation was more extensive in Tasmania and New Guinea and reached its maximum somewhat later; it had generally disappeared by some 10,000 years ago. The Australian climate (and the level of surrounding seas) has been relatively stable for the past 6,000 years. The instability of late Pleistocene and Holocene climates would have had marked effects upon the distribution of areas wherein predictably filled and unpredictably filled temporary water-bodies occurred. Such effects may have had important evolutionary consequences in that it is only in predictably filled waters that evolution (speciation) seems likely (Williams, 1984; Williams & Kokkinn, in press).

Major Drainage Divisions: Present Landforms and Climates

Brief descriptions of present landforms and climates of the major regions into which Australia can be divided on the basis of drainage patterns are appropriate to the context of this chapter. Figure 8.1 indicates the distribution of these so-called Drainage Divisions and Table 8.1 presents their areas and annual average discharges. Each division is characterized by particular sorts of aquatic habitat (e.g. the Lake Eyre Division by salt lakes and episodic creeks), but a variety of aquatic habitats is found in all divisions. The major features of Australian aquatic habitats on a general basis have been described previously (Chapter 7).

Northeast Coast Division. This division comprises those catchments of the Great Dividing Range along a broad coastal strip of Queensland from Cape York Peninsula to the southern border of Queensland. It includes peat-stained creeks and ponds in coastal dunes, some heavily forested sections between Brisbane and Fraser Island, relatively dry *Eucalyptus* forest north to Townsville and tropical rainforest interspersed with coastal plain sugar plantations between Townsville and Cooktown. Many streams are relatively short, have high initial gradients (gradually decreasing seawards), high annual discharges, seasonally variable or erratic flows and variable turbidity. Many have large estuaries with extensive areas of mangrove. In the Cape York area, there are numerous lagoons separated by areas of relatively dry forest, with rainforest sporadically present along some creeks. During the summer, flooded lagoons are inhabited by large numbers of waterfowl. During the winter and spring, these lagoons are often dry and aquatic habitats are then restricted to isolated waterholes and small permanent streams. Unfortunately, the areas of tropical rainforest are decreasing at an alarming rate because of human activities. Many animals living in them, therefore, especially those with limited distributions, are at risk.

The climate is typically subtropical to tropical, with hot, wet summers and cooler, dry winters. Annual rainfall ranges from a median of 500 mm to one of almost four metres. Summer rainfall is monsoonal and more reliable in northern regions. Winter rainfall results from southeasterly winds and is more reliable in southern regions.

Southeast Coast Division. This division comprises the seaward catchments of the Great Dividing Range from the Queensland border south through New South Wales and then west through Victoria to the mouth of the Murray River in South Australia. The region has been extensively settled so that many aquatic environments have been altered greatly by man. Even so, along the coast of New South Wales, pockets of rainforest persist and southwards these gradually give way to coastal heathlands which extend along the Victorian coast to South Australia. Dune lakes and estuaries, some large, are a frequent feature along much of the coast of this division. Away from the coast, rapidly flowing permanent streams flowing through upland meadows and often continuous forest are characteristic. Some of these streams are associated with large winter snowfields in the Snowy Mountains.

The climate is best described as warm temperate in northern areas of New South Wales and Mediterranean in southern regions of the division. Rainfall is generally reliable, with summer falls most frequent in the north, winter and spring falls commoner in the south. The range of median annual rainfall is from 1,800 mm (in the north) to <750 mm (in the south).

Tasmanian Division. Tasmania has been connected to the Australian mainland for most of its geological history and, in many respects, this division can be considered a southern

Table 8.1 Areas of and annual average discharges from major drainage divisions of Australia. (Basic data from Australian Water Resources Council)

DRAINAGE DIVISION	AREA (km ² × 10 ⁶)	AVERAGE ANNUAL DISCHARGE (m ³ × 10 ⁷)
Tasmanian	0.068	4.7
Southeast coast	0.27	3.6
Northeast coast	0.45	8.3
Gulf of Carpentaria	0.64	6.3
Timor Sea	0.54	7.4
Indian Ocean	0.52	0.61
Southwest coast	0.14	0.72
South Australian Gulfs	0.075	0.053
Murray-Darling (and Bulloo-Bancannia)	1.1	2.4
Western Plateau	1.2	0.49
Total Australia	2.7	0.0
	7.7	34.6

extension of the preceding division. Final separation from the mainland took place about 12,000 years ago. Much of the island is mountainous and forested. There is a high central plateau (1,000 to 1,200 m elevation) and several outlying upland areas. Most elevated areas were glaciated during the Pleistocene. Permanent freshwater lakes of many sizes are abundant (as well as a large number of man-made impoundments), as are rapidly flowing upland streams. A high proportion of the species of animals found in Tasmanian fresh waters is endemic to the island. A general review of the biogeography of Tasmania, with some emphasis given to aquatic environments, is given by Williams (1974).

The climate is a cool temperate one. Precipitation is high (1,500 to 3,000 mm per annum), reliable, mostly falls in winter and frequently arrives as snow.

South Australian Gulf Division. This small division encompasses an arc around the Gulf St Vincent and Spencer Gulf in South Australia. Apart from the Mount Lofty Ranges in the south and the Flinders Ranges in the north, present landforms are of moderate or low relief. There are no permanent freshwater lakes of any size. Lake Torrens is a dry saline playa. Small, intermittently filled salt lakes, however, are common in certain areas (especially the Yorke Peninsula). Streams are short and mostly temporary.

The climate is Mediterranean in the southeast and semi-arid elsewhere. Rain arrives mostly in winter. It is highest and most reliable in the southeast (median annual rainfall is 500 to 750 mm) and lowest and least reliable in the north (<150–350 mm). It is exceedingly unreliable and scanty in northwestern areas.

Murray-Darling Division. This division is inclusive of the Murray-Darling River system, the longest river system in Australia and one draining almost one-seventh of the continent. Relatively narrow eastern and southern margins include the inland catchments of the Great Dividing Range and are often mountainous and forested; fast-flowing, permanent rivers and streams are the typical aquatic habitats encountered. Elsewhere, on the plains, the division comprises flat to undulating landforms, lightly forested or grassed; long, meandering and slowly-flowing rivers, often with marginal wetlands (billabongs), are the most characteristic aquatic habitats. A great deal of river impoundment and extensive

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clearing of native vegetation for pastoralism has much altered the natural environment. Thus, over 90% of the exploitable water resources of the division are now committed and the Murray River is impounded from headwaters to mouth.

A wide range of climates is shown within this division. It ranges from cool temperate in upland regions where the headwaters of the major rivers arise, to warm and semi-arid on the plains through which they mostly flow. Median annual rainfall in the uplands may reach over 1,500 mm, is reliable and falls mostly in winter. On the plains, rainfall is less than 400 mm per annum and falls more unreliably.

Lake Eyre and adjacent internally drained Divisions. This large area of endorheic (internal) drainage covers much of the semi-arid and arid eastern half of the continent. Its typical landforms are featureless desert plains, low-lying hills and longitudinal dune systems. Desert vegetation predominates, but *Eucalyptus* and *Melaleuca* species occur near the few permanent or almost permanent watercourses. Large and usually dry salt lakes and episodically-flowing streams and rivers are the most obvious aquatic habitats of these divisions, but permanent mound-springs and isolated waterholes also occur. Shallow, temporary fresh or saline lakes are obvious aquatic habitats after sudden downpours.

The climate is uniformly arid to semi-arid. Rainfall is low (the median annual value is <300 mm) and unreliable. In northern regions, it is often associated with monsoonal systems. Sudden downpours may occur throughout the region, however, and dramatically flood and transform the landscape.

Western Plateau Division. This large area of uncoordinated drainage covers almost one-third of the continent and all the arid western half. A few small plateaux and isolated areas of high ground occur, but the most common landforms are flat, sandy or stony plains covered by low scrub, shrubs or desert grasses. Surface waters are rare; most are extremely temporary and found only after erratic rain has fallen. Episodically filled salt lakes, claypans and short watercourses are, therefore, the most widespread types of aquatic habitats. A few, small, isolated and permanent freshwater bodies occur sporadically where topographic conditions are suitable.

The climate is arid and rainfall low (median annual values are between 100 and 350 mm) and erratic in distribution. When rain does fall, it does so mostly in summer.

Southwest Coast Division. This division includes those areas drained by a number of rivers which flow to the Indian and Southern Oceans between Geraldton on the western coast and Esperance on the southern coast. Inland, the division covers the southwestern extremity of the Western Plateau or Shield, but the most obvious topographic feature of the division is the Darling Escarpment which represents the abrupt western edge of the plateau. Below the escarpment is a wide, sandy coastal plain. Grassland and lightly forested areas inland are replaced towards the southwestern corner by thick *Eucalyptus* forest. Permanent streams are common and seasonally-filled salt lakes are frequent in local, endorheically drained areas. Inland, streams often become saline, especially in summer (Hodgkin *et al.*, 1979). Most permanent streams are narrow and often have dark, peat-stained water. In upland regions, the streams are well shaded and flow through forest; near the coast they generally flow through open heathland. Most of the larger streams (Swan, Murray, Blackwood) have extensive estuaries. Streams are scarce and small in areas north of Perth and east of Albany.

The climate is temperate. Summers are warm and dry, winters cool and wet. Rainfall is least inland (where the median annual value is about 250 mm) and greatest and most reliable near the coast (1,400 mm).

Indian Ocean (or Pilbara) Division. This division covers those river systems draining the central western coast of Western Australia. Much of the topography is rugged with a terrain of many deeply dissected plateaux covered with low scrubs and with many gorges. Near the coast, the terrain flattens to a sandy plain. Relief is also low in the southern part of this division. The most characteristic type of aquatic habitat is that provided by intermittently flowing streams or rivers. Pools along the courses of some of the rivers, particularly inland, may be permanent. Waters, for the most part, are fresh, but some rivers draining off the western edge of the Western Australian Plateau may be saline.

The climate is generally arid and subtropical, though a more Mediterranean-like climate prevails in the southern part of the division. Rainfall is low and unreliable; nowhere is the median annual value in excess of 400 mm. In the north, rain is usually associated with summer cyclones or monsoons, whereas in the south it is usually associated with winter low pressure systems.

Timor Sea Division. This drainage division includes the Kimberley Plateau and regions marginal to it in the far northern part of Western Australia and the more dissected plateaux of the northern part of the Northern Territory. Overall, the topography is dominated by dissected tablelands and ridges, often rugged, interspersed by - and giving rise on the coast to - flat alluvial plains. Lakes are rare and the most important aquatic habitats are permanent rivers and associated wetlands which flood in summer and cease to flow in winter when they dry to a series of isolated pools (sometimes large). Perhaps nowhere else in Australia are seasonal hydrological conditions so important a determinant of the nature of aquatic environments. Williams (1983) refers to such habitats as "northern flood-drought rivers".

The climate is tropical. Summers are hot and wet, winters warm and dry. Rain is monsoonal or associated with tropical cyclones. Median annual rainfall varies from about 1,500 mm in the north to less than 400 mm in the south.

Gulf of Carpentaria Division. All river systems discharging into the Gulf of Carpentaria are grouped into this drainage division. Thus, it includes the coastal rivers of the northeastern part of the Northern Territory and of northern Queensland. Topographically, there is a broad coastal plain which rises inland to Arnhem Land and the Barkly Tableland in the west and south and to the northern part of the Great Dividing Range in the east. These uplands are deeply incised by rivers, but the coastal plain is very flat. Because of low gradients on the coastal plain, saline water may penetrate large distances inland along the rivers. Relatively large, intermittently flowing rivers are the most characteristic form of aquatic environment; most have extensive deltas and tidal flats near their mouths. Some of the smaller creeks, especially in upland regions, may be permanent.

As in the Timor Sea Division, the climate is tropical, with hot, wet summers and warm, dry winters. Rainfall is large in northern regions; in some places the median annual value is more than 1,500 mm. It is less in southern regions, where the comparable value may only be 300 mm. Most rain is associated with the summer monsoons or tropical cyclones. Only after such events, of course, do rivers begin to flow.

ORIGINS

Clearly evident from the preceding Section, the aquatic fauna of Australia has developed on a continent whose position over geological time has undergone significant change with respect to other continents, which has been isolated from other landmasses for long periods, and whose climate has

fluctuated greatly. Also evident is that the continent has now, and probably has always had, a wide variety of aquatic habitats. Not surprisingly, therefore, the aquatic fauna is thought to have originated from several sources. Lack of fine-grained palaeoclimatic information, palaeontological evidence and a detailed knowledge of the phylogenetic systematics of most aquatic groups preclude a complete analysis of faunal origins at present. Nevertheless, important generalities can be recognized; five (or six) sources clearly have been important in the derivation of the aquatic fauna.

First, an important source has been the ancient Gondwanan fauna. Close phylogenetic relationships occur between several aquatic groups presently found in waters of South America, South Africa, Madagascar, New Zealand and Australia. Such groups are particularly common in the upland waters of southeastern Australia (including, especially, Tasmania). The existence of these amphinotic (circum-Antarctic) relationships can only be adequately explained by accepting that the groups involved had a common Gondwanan origin.

Second, southeastern Asia clearly has provided another important source for the Australian aquatic fauna. The co-occurrence of many species in northern Australian fresh waters and in waters of the Indonesian archipelago, or at least close relationships between many northern Australian forms and southeastern Asian forms, points to the importance of Asia in this respect. Southeastern Asia has been, of course, most important with regard to the derivation of the fauna of northern Australia, but its influence is not restricted to northern waters alone; several animals of reasonably certain Asian origin occur far southwards.

The sea represents a third source. Possibly this environment has been relatively more important in Australia than elsewhere. Certainly, a rather large number of Australian faunal groups can be plausibly derived from marine ancestors. At least two waves of marine immigration seem to have occurred: an ancient one which produced animals now found in completely fresh waters well inland and a more recent one which produced groups still confined to fresh or slightly saline waters near the coast.

The terrestrial environment is a fourth source. It has not been an important one, but at least one good example exists of a species now quite aquatic, but easily derivable from a terrestrial ancestor.

Rather more important, and a fifth source, are inland waters of the Northern Hemisphere and conterminous landmasses. Such waters are inhabited by several groups of easily dispersed aquatic animals which have spread to Australia (or whose distribution, in any event, includes Australia). The proportion of the aquatic fauna of Australia now regarded as belonging to such cosmopolitan groups is much less than was thought to be the case.

Perhaps a sixth source, *Homo sapiens*, should also receive mention, for there is no doubt that the large number of aquatic exotics which now maintain viable populations in Australia and which have been introduced either accidentally or intentionally, comprise a significant element of the modern fauna. Unfortunately, their significance is set to increase.

As noted, the origins of all groups of the aquatic fauna of Australian inland waters cannot yet be determined with confidence. To provide substance to our general remarks above, however, some brief comments on the origins of all groups will not be out of place – though in many cases they rest more on plausible speculation than firm evidence. The groups are considered on the same taxonomic basis as in Chapter 7.

Lower Invertebrate Phyla

As previously indicated (Chapter 7), most protozoan genera are cosmopolitan. Many species also appear to be of worldwide distribution. Modern research, however, now suggests that, at least at the species level, cosmopolitanism is much less common than was thought to be the case.

Most Australian freshwater sponges (Spongillidae) seem to be of Asian origin, although at least one genus appears to have evolved in Australia and two species may have been introduced recently (Penney & Racek, 1968).

Members of the Cnidaria in Australian inland waters seem to have had a variety of origins. Some hydroids (Hydridae) are cosmopolitan. At least one, however, may have evolved here. Marine origins are indicated for species of *Cordylophora* and for *Craspedacusta sowerbyi* (though perhaps not locally in both instances) as well as for the endemic Australomedusidae (of almost certain local marine origin).

Pseudocoelomate and Acoelomate Phyla

At present, little of substance can be said about the origins of the Australian freshwater Turbellaria. There is no doubt, however, that further studies of this group have much to offer biogeographers. Turbellarians are fragile creatures which lack any desiccation-resistant stages in their life cycle. They are clearly propitious animals for biogeographical study. Studies thus far have attempted to explain current biogeographical patterns on the basis of continental drifting (Ball, 1975). Certainly, a Gondwanan origin seems likely for at least those forms confined to upland areas of southeastern Australia. The Dugesiidae, a family which attains its greatest diversity in the Southern Hemisphere (and especially in Australasia), is known to contain some very primitive species in Australia.

Gondwana also may have been involved in the origin of the temnocephalids, for these, like the Dugesiidae, are most abundant and diverse on landmasses of the Southern Hemisphere. Temnocephalids, however, also occur in Europe and Asia so that their origin and spread obviously cannot have been a simple affair.

Gondwana does not seem to have played any significant role in the origins of the other acoelomate group (Nemertea) nor most, if not all, of the pseudocoelomate groups occurring in Australian inland waters (nematodes, nematomorphs, gastrotrichs and rotifers). The only nemertean species recorded from Australia, *Prostoma graecense*, occurs widely on other continents; Gibson (1972) suggests that it may well have been dispersed by man or on the feet of migrating waterbirds. Whatever the case, there is no doubt that the origins of the freshwater Nemertea lie in the marine environment. Moore & Gibson (1973) suggest that the route followed from this environment led through estuarine and brackish waters. Little can be said about nematode origins; most Australian genera and many species are likely to prove to be widespread or cosmopolitan forms whose origins lie outside Australia (Nicholas, 1975). The same may also apply to Australian gastrotrichs, perhaps the nematomorphs and certainly most rotifers. So little is known about the gastrotrichs and nematomorphs, however, that so far as this statement applies to those groups it is no more than plausible speculation. Much more is known about the rotifers. Whilst many species of these (and all rotifer genera) are indeed cosmopolitan, a large fraction of the fauna has restricted distributions. Thus, rotifer assemblages of northern Australia have clear affinities with the Indo-Asian fauna and include a pantropical component (Shiel & Koste, 1986). Additionally, some Tasmanian species have disjunct and anomalous dis-

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tributions; several are also pantropical. About 15% of the Australian rotifer fauna is endemic at the species level and may thus be considered to have originated in Australia.

Coelomate Phyla other than the Arthropods and Vertebrates

Only a single species of the Bryozoa appears to be endemic to Australia; the rest are either cosmopolitan or occur on at least one other continent. Given the ability of the group to produce resistant and easily dispersed reproductive bodies (statoblasts), such a situation is not unexpected. For the most part, then, the Bryozoa of Australian inland waters can be considered as having originated outside the continent and, since the overwhelming majority of bryozoans is marine, from marine ancestors (though phylactolaemates, which include most freshwater bryozoans, are generally considered to be the most primitive of living Bryozoa).

Little of substance can be written about the origins of Australian tardigrades. If species endemicity is as high as certain authors claim for this group, then many species presumably have arisen here.

According to Smith & Kershaw (1979), the present freshwater snail fauna of Australia has two ancestral sources: Gondwana and Asia. At least one other source, however, can be identified: the marine environment. Additionally, at least some snails are anthropochorous exotics. Snails which originated from Gondwanan ancestors include those in the extremely diverse Hydrobiidae; those which originated from Asian ancestors include the Lymnaeidae, Planorbidae and Viviparidae (Smith & Kershaw, 1979). Snails of obvious marine derivation include species of Neritidae and Iravadiidae. Species of *Physa* (Physidae) are recent introductions.

The origins of the Australian freshwater mussel fauna are clouded and speculations about them and patterns of mussel dispersal have involved variously the Northern Hemisphere, Gondwana and the Indo-Pacific region (Walker, 1981). Even so, many zoogeographers allege a close relationship between the mussel faunas of Africa, South America and Australasia (e.g. Parodiz & Bonetto, 1963). Of particular significance in this regard is the co-occurrence of the Hyriidae in Australasia and South America. The only Australasian mussels which may not belong to the Hyriidae are those in the genus *Haasodonta*; this New Guinea genus may prove to have affinities with the predominantly northern Unionidae and, if so, recent immigration from southeastern Asia is suggested. Whatever the case, the high species endemicity of the Australian mussel fauna and the fact that the mussel faunas of New Zealand and Papua New Guinea are clearly of Australian origin, points to the continent as a major region of mussel speciation. The other two groups of bivalve molluscs found in Australian fresh waters, namely the Sphaeriidae and Corbiculidae, contain widespread and more or less cosmopolitan species. Australia apparently has not played a significant role in their evolution.

The few, free-living polychaete annelids found in Australian inland waters are restricted to coastal situations and are clearly of local marine derivation. *Stratiotrilus*, an ectoparasitic polychaete found in the gill chambers of certain freshwater crayfish, has not originated in this fashion. Its origins appear to lie with an ancient Gondwanan fauna as its present distribution encompasses South America, Madagascar and Australia.

A Southern Hemisphere distribution also is shown by some oligochaete annelids, particularly the Phreodrilidae, so that for these, too, an ancient Gondwanan fauna provided ancestors. By no means all oligochaetes show a southern pattern of distribution implicating Gondwana as a place of

origin. Some Australian aquatic oligochaetes are probably aquatic immigrants from local terrestrial ancestors (Megascolecidae); others represent cosmopolitan or widespread forms that have spread to Australia (e.g. some Naididae). Others clearly have been introduced by man (e.g. Lumbriculidae and Lumbricidae).

The leeches (Hirudinea) manifestly have evolved from the oligochaetes, but there is no certainty at present from which group they arose. Nevertheless, the structural homogeneity of leeches strongly indicates a monophyletic origin and, in view of their ubiquity (though not all families are equally dispersed), the group most probably evolved outside Australia. Within Australia, however, leeches have a high degree of generic endemicity, with one diverse family, the Richardsoniidae, almost endemic. A certain degree of adaptive radiation apparently has occurred in this family within Australia. Other Australian families are less diverse and contain at least some genera that are widespread or cosmopolitan and probably evolved elsewhere.

Arthropods: Arachnids and Crustaceans

The spiders associated with Australian inland waters are derived, or so it would most plausibly seem, from local terrestrial ancestors. One species, however, as yet undescribed, seems to have originated from local intertidal spiders; it occurs, apparently amphibiously, in South Australian coastal salt lakes (Williams, 1984). Hydracarine arachnids include several endemic genera of likely local origin as well as several widespread or cosmopolitan genera. Some genera confined to South America and Australia are also represented. The Australian hydracarine fauna has evolved from several sources.

The discussion here of the origins of the crustacean fauna of Australian inland waters largely follows Williams (1981). More general accounts of crustacean origins are given by Cisne (1982) and Schram (1982). An important initial point to note is that a wide range of dispersal abilities occurs within the group. Thus, some branchiopods have small, resistant and easily transportable eggs. No malacostracans, on the other hand, have eggs of this type, and most malacostracans cannot withstand desiccation; malacostracans clearly do not have high dispersal abilities. Malacostracans living in restricted underground waters have extremely poor dispersal opportunities.

Within the Anostraca, *Artemia "salina"* is probably a widespread exotic form recently introduced (see discussion in Geddes & Williams, in press), but all other Australian anostracan species are endemic. Of the two genera involved, one, *Branchinella*, is distributed worldwide and seems to be a very old genus which originated outside Australia and which on reaching the continent underwent an adaptive radiation (Geddes, 1983). The other genus involved, *Parartemia*, is endemic and its ancestors are of uncertain provenance. The geographical movements of predictably and unpredictably filled salt lakes into different climatic zones in response to palaeoclimatic fluctuations have been suggested as an important speciating mechanism within the genus (Williams, 1984).

Of the notostracans present in Australia, *Lepidurus apus* is more or less cosmopolitan; it is perhaps one of the most widespread of all crustaceans (Abele, 1982). A distinct subspecies, *L. apus viridis*, however, has been described from Australasia. To determine from where the species itself arose is not possible. The other notostracan present, *Triops australiensis australiensis*, presumably arose in Australia, since this taxon is endemic to the continent. The only other subspecies, *T. australiensis sakalavus*, occurs on Madagascar, to which island it seems likely that the parent species was carried by the southeastern tradewinds. That the affinity of Australia and Madagascar in this respect reflects any Gondwanan

connection is unlikely. Although the extended geographical distributions and low species diversity of notostracans on a world basis clearly support the view that poor geographical separation constrains notostracan speciation, recent work (see Abele, 1982) suggests that diversity in this group of crustaceans is not as low as was previously thought, that some species at least have rather restricted distributions and, concomitantly, that the eggs of some species may not be dispersed easily.

Conchostracan origins, so far as representatives of the group in Australia are concerned, appear to have involved an adaptive radiation at the species level once genera widespread outside Australia had reached the continent. The lack of effective geographical barriers (small, resistant eggs are produced) has perhaps constrained the extent of this radiation. This pattern of distribution (widespread genera with few cosmopolitan species) seems to be a general and very old character of conchostracans; continental drifting has been invoked to explain generic distributions (Tasch, 1979).

According to Smirnov & Timms (1983), Australian Cladocera comprise five major groups with respect to distributional relationships and hence origins. There is a cosmopolitan group of species which, although not as important as was previously thought, is nevertheless a significant group overall. Then there is a group of widespread but not cosmopolitan species; many species here are circumtropical and are especially common in northern Australia. Bird migration and wind are likely dispersal agents for these two first groups. Migrating birds are also likely dispersal agents for the third group of species, those displaying essentially bipolar distributions; such species occur in the Palaearctic and Australia. A fourth group includes those species of Gondwanan affinities, though few of those involved occur now on all "southern" continents (including India). *Daphniopsis* provides an example for this group of particular interest because, in addition to its wide distribution in the Southern Hemisphere (it has recently been reported from South America; Hann, 1986), it also occurs in Tibet and China and this Asian distribution has been used to suggest that Gondwana included a larger fraction of Asia than most geologists believe (Crawford, 1974). The species diversity of *Daphniopsis* in Australia is now thought to be relatively large (see Kokkinn & Williams, 1987) and this diversity, as perhaps for *Parartemia* (see above), may reflect movements of predictably filled and unpredictably filled salt lakes in response to secular climatic fluctuations. A fifth group includes old endemics of mostly uncertain original derivation.

Most ostracods, unlike cladocerans, do not have drought-resistant eggs. Ostracods, correspondingly, are not so easily dispersed and the greater role that Gondwana seems to have played in the origin of the Australian ostracod fauna can be best interpreted on this basis (McKenzie, 1971). Certainly, low dispersal ability offers a ready explanation for the high diversity and marked endemicity of ostracods in Australian inland waters. De Deckker (1983) explores further than can be done here zoogeographical patterns of non-marine species in Australia.

Many copepods do produce drought-resistant eggs, but there is increasing evidence that these are not necessarily easily dispersed (and certainly not as easily as was thought by earlier biologists). On this basis, it is not surprising that Gondwanan origins are also regarded as important for several copepodan groups, especially the centropagid calanoids. Some harpacticoids (*Attheyella*) provide further examples. In addition to Gondwana, however, several other origins are seen as important for particular sorts of copepod. The distribution of the Diaptomidae (Calanoida) clearly indicates that southeastern Asia has been an important origin for some species. The occurrence of several cosmopolitan or widespread cyclopoid

species points to the importance of a wider origin for others. The marine environment is viewed as an important source for many salt lake harpacticoids.

Finally, with regard to entomostracan crustaceans, Australian branchiurans are thought to have originated either on Gondwana (*Dolops*; Fryer, 1969) or elsewhere and reached Australia other than by continental drift (*Argulus* spp.).

No Australian malacostracans are cosmopolitan or widespread species, but they are otherwise as diverse in origin as the entomostracans. Three sources are seen as important: Gondwana, southeastern Asia (and beyond) and the marine environment. A fourth source, the terrestrial environment, is less important.

Malacostracans of likely Gondwanan origin are the phreatoicid isopods, the parastacid crayfish and the amphipod family Amphiniscidae. All have distributions which, in addition to Australia, include some other (though not all other) southern landmasses. Some Australian freshwater amphipods also may have originated from stocks associated with Gondwana (cf. Williams, 1986a), but the relationship remains problematical. Early thoughts were that at least the corophiid and crangonyctoid species were of Gondwanan derivation, but recent investigations indicate that, aside from the close relationship of Australian crangonyctoids and *Paramelita* in South Africa, crangonyctoids in Australia show no unique distinctions from similar groups on other continents. Whatever the role of Gondwana in the origin of the crangonyctoids, Australia appears to have been a major evolutionary centre and refuge for freshwater amphipods (Barnard & Karaman, 1983).

Malacostracans whose probable origins lie in southeastern Asia are the sundathephilusid crabs, bathynellacean syncarids and the atyid and palaemonid shrimps (*Macrobrachium* only). The crabs have been suggested to be the last to arrive; the late Tertiary has been proposed. The Madagascan and African affinities of some Australian cave atyids (*Parisia*) remain anomalous in this context; perhaps these atyids are Gondwanan relicts.

Malacostracans of certain and probably relatively recent marine derivation are the anthurid, sphaeromatid and cirolanid isopods, *Palaemonetes* spp. (palaemonid shrimps) and crabs of the families Grapsidae and Hymenosomatidae. Those of less certain and older marine derivation are the janirid isopods and cenid and eusirid amphipods.

Haloniscus, an oniscoid isopod, has been derived from local terrestrial ancestors.

Arthropods: Insects

The affinities of most Australian aquatic insects lie either with the insect fauna of other landmasses of the Southern Hemisphere, or with the insect faunas of southeastern Asia and especially the Indonesian archipelago. Thus, two important elements can be distinguished (Mackerras, 1970): an old southern element of Gondwanan affinities and a younger northern one with Oriental or Indo-Malayan affinities. The former element includes many endemic genera, whereas the latter has radiated rather little above the species level. Additionally, two other elements can be distinguished which are less important: a cosmopolitan element and a uniquely Australian one.

Examples from many Australian aquatic insect orders can be recognized as relatives of insects on other southern landmasses.

All Australian stoneflies have such affinities. Early phylogenetic analysis of the order (Illies, 1965) confirmed the Gondwanan relationships within the faunas of South America,

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Australasia and South Africa. Several (but not all) mayfly families, likewise, have been shown to have Gondwanan affinities (e.g. Siphlonuridae, Oligoneuriidae, Leptophlebiidae), as do several caddisfly families. Of other insect orders with clear Gondwanan affinities, special mention should be accorded the dragonflies; about one-third of all Australian species are said to have had a Gondwanan origin. Families particularly involved here are the Chlorolestidae and parts of the Aeshnidae and Gomphidae. Important dipteran genera with Gondwanan affinities are *Austrosimulium* and *Cnephia* (Simuliidae) and several chironomid genera, especially within the subfamilies Podonominae and Aphroteniinae. *Archichauliodes* is a megalopteran genus of Gondwanan affinity; the Nannochoristidae, a family of the Mecoptera, has similar affinities.

With regard to those aquatic insects of northern affinity, mention is made of the prosopistomatid and ephemerellid mayflies and several caddisfly families, especially the hydropsychids and leptocerids. Over one-third of dragonfly species have northern affinities and in this matter the families Coenagrionidae and Libellulidae are particularly important. Of dipterans, the Blephariceridae and several culicine genera are of northern affinity, as also, it seems, are most Australian aquatic bugs (but not *Diaprepocoris* which appears to be an ancient southern form).

Aquatic insects that are essentially of cosmopolitan affinity include baetid and caenid mayflies and a rather large number of dipteran genera. Among the latter may be recorded *Simulium* (Simuliidae), several chironomid genera (as *Chironomus*), many ceratopogonid genera (as *Culicoides*) and some culicid genera (as *Culex*).

Part of the small, uniquely Australian element amongst the aquatic insects are the families Chathamiidae and Plectrotarsidae in the Trichoptera.

Fishes

There is little direct (*i.e.* fossil) evidence on the origins of the present freshwater fish fauna. With the exception of the Queensland Lungfish (*Neoceratodus forsteri*) and the osteoglossid *Scleropages* (two species), which clearly have Pangaean-Gondwanan affinities, our knowledge of the origin of most Australian groups is based solely on zoogeographic evidence. A Gondwanan origin seems a distinct possibility for at least another five families: Retropinnidae, Prototroctidae, Galaxiidae, Aplochitonidae and Percichthyidae. The relationships and origins of these families, particularly the Galaxiidae, have been the subject of heated debate (McDowall, 1964; 1970; 1971a;b; 1973; 1978; McDowall & Whitaker, 1975; McDowall & Gosztonyi, 1975; Rosen, 1974; Croizat *et al.*, 1974; Ball, 1975). Most of these groups contain species that spend part of their life at sea and it is not clear if their present austral distribution is the result of marine dispersal or Gondwanan vicariance. The Percichthyidae as treated here includes elements previously considered as serranids, kuhliids and gadopsids (Johnston, 1984). The group appears to be restricted to fresh waters of Australia and South America.

Few Australian species have northern or Oriental freshwater origins. The persistent, deep oceanic barrier between eastern Indonesia and the Australia-New Guinea region has prevented dispersal of the rich cypriniform-siluriform dominated fauna of southeastern Asia from reaching Australia. The synbranchid eels and one ambassid (*Parambassis*), however, may be exceptions that have negotiated this barrier. In the case of the synbranchids, the possibility of a Gondwanan origin cannot be discounted (Rosen, 1976).

The largest element in the fauna is composed of secondary freshwater species derived from marine ancestors, probably about the time Australia achieved its present geographic position or afterwards. About 70% of the inland species have strong affinities with tropical Indo-Pacific marine fishes. Prominent in this category are the Ariidae (five species), Plotosidae (12), atheriniforms including Atherinidae (nine), Melanotaeniidae (13), and Pseudomugilidae (six), Teraponidae (22), Eleotridae (25) and Gobiidae (12). The Australia-New Guinea region is particularly notable for its freshwater radiation within groups that elsewhere are almost entirely marine or estuarine: for example, the ariiid and plotsid catfishes, teraponid grunter, eleotrid gudgeons.

Finally, mention should be made of the salamanderfish (*Lepidogalaxias salamandroides*), a diminutive pond and swamp species of southwestern Australia. Its relationships and origins remain obscure, although it appears to be an extremely old relict of Gondwanan or Pangaean ancestry. Limited osteological evidence indicates possible relationships with Northern Hemisphere Esocidae (Rosen, 1974). Comparative electrophoretic and morphological studies currently in progress, it is hoped, will clarify its taxonomic position.

Amphibians

Until recently, Australian amphibians were believed to be wholly derived from Oriental relatives (Darlington, 1965). This viewpoint, however, is untenable in the light of modern concepts of continental drift and an increased taxonomic knowledge. Indeed, with the exception of the single species of Ranidae whose Oriental affinities are clear, the majority of the Australian fauna (Hylidae and Myobatrachidae, or about 94% of the species) appear to have evolved from southern ancestors. This segment of the fauna is most closely related to South American frogs, thus providing evidence of a common Gondwanan origin. The origins of the remaining Australian family, the Microhylidae, is controversial. The group is represented on all major continents, but with highest diversity in New Guinea (13 genera and 102 species). Savage (1973) suggests Australia as the centre of origin, but Tyler (1971) postulates that Australia was colonized by microhylids via New Guinea during the Pleistocene.

Reptiles

Most of the Australian reptile fauna appears to have Oriental affinities, with ancestral forms having reached the continent during the Tertiary and then undergoing extensive adaptive radiation (Cogger & Heatwole, 1981). The freshwater tortoise family Chelidae, however, is shared with South America and its distribution is indicative of a Gondwanan origin (Burbidge *et al.*, 1974). Ancestral forms have been present in Australia since at least the Cretaceous, prior to the onset of widespread aridity.

Birds

Because of a patchy fossil record, an ability to fly over oceanic barriers and the present widespread distribution of many groups, the origins of most Australian birds remain uncertain. Few fossils are known from pre-Miocene times, but by the mid-Miocene a moderately diverse assemblage of modern families were present (Rich, 1975). Mayr (1944) believes that the Australian fauna originated from a succession of colonizations from northern areas, mainly southeastern Asia. This idea, however, has been modified with the acceptance of continental drift. Even so, the bulk of Australia's waterbird fauna probably entered from the Indo-Malayan region (Rich, 1975). Orders which appear to have uti-

lized this route include Podicipediformes, Pelecaniformes, Ciconiformes, Gruiformes and most Charadriiformes. The origins of some cosmopolitan forms such as pelicans and cormorants are nebulous at best. Quite possibly, they entered Australia via oceanic dispersal.

Although many Australian Anseriformes (waterfowl) are closely related to and derived from northern groups, a southern or Antarctic dispersal route cannot be discounted for at least some. Such an entrance seems likely for the ancestors of the more primitive anatids including the Anseranatinae (Magpie Goose) and *Cereopsis* (Cape Barren Goose). There is also a possibility that the Recurvirostridae (avocets and stilts) has southern affinities (Rich, 1975), but an Indo-Malaysian dispersal route is equally probable.

Orders which are primarily terrestrial, but contain at least some members closely associated with estuaries or inland waters, include the Falconiformes, Galliformes and Coraciformes. The "aquatic" species in these groups, for example sea eagles, ospreys, the swamp and marsh-frequenting King Quail (*Coturnix chinensis*) and the several species of kingfisher, all appear to have entered Australia from the north.

Mammals

Unfortunately, the origin of Australian monotremes remains obscure, due mainly to the paucity of knowledge about Early Cretaceous mammals on other continents. Although fossil monotremes are known only from Australia, the possibility that monotremes occurred elsewhere during the Cretaceous cannot be excluded (Archer *et al.*, 1985).

There are no extant aquatic marsupials in Australia.

The water rats apparently originated in New Guinea from where they colonized Australia (Ziegler, 1982). Although their time of arrival is uncertain (recent evidence suggests the Pliocene), ancestors of the native water rats were probably amongst the first of the Muridae to colonize Australia. The Water Buffalo (*Bubalus bubalis*) was introduced from southeastern Asia between 1825 and 1829.

ADAPTATIONS

Adaptations to life in Australian inland waters comprise: (1) those which are general adaptations enabling animals to live in inland waters and essentially similar to those of aquatic animals worldwide; and (2) those which are particular adaptations of the fauna to features especially characteristic of the Australian inland aquatic environment, namely the ephemeral or temporary nature of many waters, high salinities and the marked hydrological fluctuations of many rivers and streams.

Given the overall aims of this Volume and the constraints of space, a discussion of general adaptations is not proposed; for comprehensive discussion of this matter, reference should be made to other accounts (e.g. that of Hynes (1970) for adaptations to life in flowing waters). Discussion in the present account is restricted to particular adaptations.

For the most part, although most obvious in Australia, the sorts of adaptations to be discussed are those possessed by aquatic animals of other arid and semi-arid regions of the world. These adaptations, however, unlike general ones, have been the subject of relatively few reviews, though the review by Williams (1985) on the nature of biotic adaptations to temporary standing waters in arid and semi-arid regions is of some value in this respect. Since this account draws heavily upon Australian examples, it has provided a useful basis for the present one.

The nature of individual adaptations to the stresses posed by ephemerality, high salinity and marked hydrological change cannot be considered in isolation because more than one of these stresses frequently occurs contemporaneously. An obvious example of a habitat in which this occurs is an ephemeral salt lake. Animals living in such habitats must possess adaptations not only to cope with the ephemerality of their milieu but also its fluctuating and high salinity (in addition, of course, to other stresses such as high light intensities, elevated temperatures and low oxygen concentrations).

Natural selection of the fauna of Australian inland waters, therefore, has produced a fauna with a series of adaptations to a variety of environmental stresses, some or many of which may occur contemporaneously or sequentially. Only the most important of these adaptations are discussed below. For convenience, the account takes the form of comments on adaptations to individual stresses, but the multidimensional nature of requisite adaptations should be remembered at all times. To add perspective, the individual accounts are prefaced by general comments on the nature, distribution and significance of ephemeral, saline and hydrologically variable waters in Australia.

Adaptations to Ephemerality

There are many water-bodies in Australia, both standing and flowing, which permanently contain water (or at least do so for several years). Throughout the semi-arid and arid regions of Australia (by far the most widespread climatic regions of the continent), however, seasonal or episodic water-bodies are the most characteristic and dominant limnological feature. Some mention has already been made of temporary water-bodies (Chapter 7). The variety of such bodies must be emphasized for the present discussion. The most important include wetlands containing fresh water seasonally, temporary salt lakes, rainpools, rock puddles, episodic streams and rivers and, on river floodplains, billabongs that fill only after exceptionally high river floods.

Three main factors seem to determine the nature of the fauna of ephemeral waters: salinity, the extent to which the locality in question is or is not associated with flowing waters and the predictability (regularity) in the occurrence of water. These three factors have been used to provide a classification of temporary waters in semi-arid and arid regions (Williams, 1985).

Although this classification primarily was intended to apply to standing waters alone, it is easily applied to flowing waters. It may usefully be reproduced here. Six categories of temporary water-body are distinguished, as the following examples of each indicate:

Predictably filled water-bodies

Fresh waters

Discrete e.g. rain pools [1]

Associated with flowing waters e.g. seasonal wetlands on riverine flood-plains, temporary streams flowing seasonally [2]

Saline waters e.g. seasonally filled salt lakes [3]

Unpredictably filled water-bodies

Fresh waters

Discrete e.g. claypans in arid regions [4]

Associated with flowing waters e.g. episodic streams [5]

Saline waters e.g. ephemeral salt lakes in arid regions (Lake Eyre is the best-known example) [6]

8. AQUATIC FAUNA ORIGINS

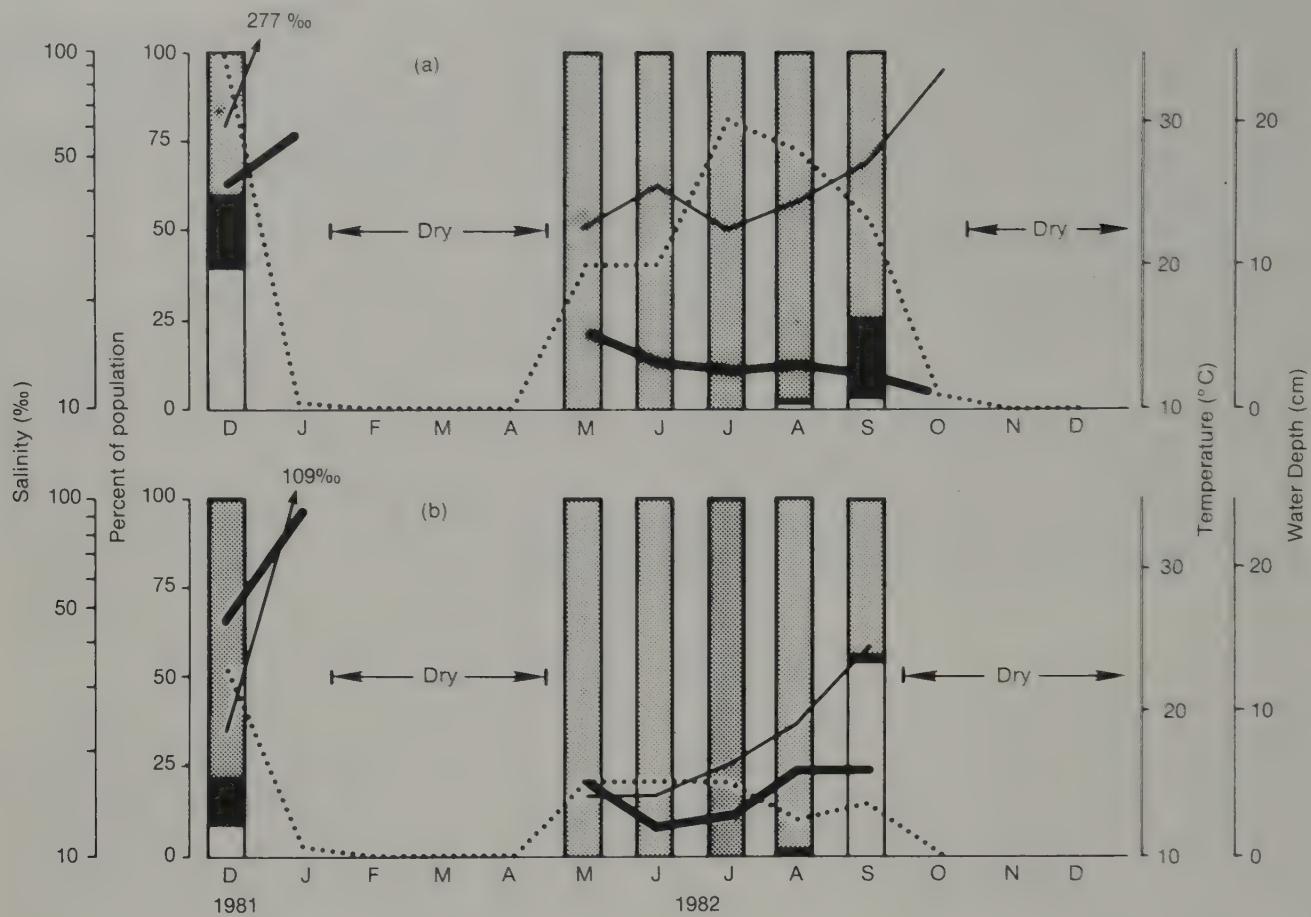


Figure 8.2 Life cycle of *Daphniopsis* cf. *pusilla* in two salt lakes in southeastern South Australia. (a) Lake Cantara North; (b) Coxiella Lake. Proportions of parthenogenetic females (stippled), ephippial females (open) and males (black). Salinity shown as thin line, water temperature as thick line and water depth as dotted line. (After Williams, 1986b)

[R. Evans]

All six categories are widespread and common over large tracts of Australia where they are often important landscape features. In our view, with the particular exception of Gondwanan faunal elements, the diversity and distribution of the fauna of Australian inland waters has been moulded to a significant degree by the need for ancestral forms to have been able to withstand long periods of aridity (see, for example, De Deckker, 1986). In other words, the ephemerality of many waters in Australia has been a potent selective force in the evolution of the present fauna.

Of particular significance in this matter have been secular climatic fluctuations. These have caused gross changes in the distribution of areas where predictably filled or flowing waters have occurred and thus brought about geographical separation of populations, the usual prerequisite for speciation. Speciation seems likely to have occurred only in those water-bodies which predictably (regularly) contained water (see Williams, 1984, for further discussion). The broad evolutionary pathway, therefore, was: fauna of permanent waters → fauna of predictably filled waters → fauna of unpredictably filled waters.

As for the sort of adaptation which must have evolved in the first of these steps, that is, before the occupation of any temporary water-body, three main sorts clearly are needed. Adaptations are needed to withstand the dry season; life cycle adaptations are required; and adaptations to provide for adequate dispersal must arise. All three sorts of adaptation

are often linked, of course. The development of special dispersal abilities is the factor which has enabled the occupation of unpredictably filled waters.

The need to survive the dry phase has produced adaptations at either the egg, juvenile or adult stage. Crustaceans provide the more obvious examples of animals which survive the dry phase by producing eggs resistant to desiccation. Thus, many of the more common entomostracans of Australian salt lakes produce resistant eggs. A frequent pattern is for large numbers of non-resistant eggs to be produced during favourable environmental conditions, and then fewer and resistant eggs at the onset of unfavourable conditions. This pattern is clearly shown by *Daphniopsis pusilla*, a cladoceran found in mildly saline Australian lakes, though the precise environmental cues, it may be noted, have yet to be isolated (Fig. 8.2). A few crustaceans produce resistant cysts containing embryos at an arrested state of development. *Mesochra baylyi*, an harpacticoid found in salt lakes of eastern Australia, does this.

Survival as resistant larvae is an adaptation to ephemerality displayed by several insects, notably the chironomids. Larvae of *Allotrichoscladius amphibius* for example, a species found in temporary fresh waters in Western Australia, can survive for considerable periods in an almost dehydrated state. This species, as well as several other Australian chironomids, also develops a protective larval capsule which can resist desiccation for lengthy periods. The occurrence of truly cryptobiotic chironomid species in Australia has yet to be demonstrated. So far as we know, no Australian species has the remarkable

capacity possessed by *Polypedilum vanderplanki*, an African species, of being able to undergo complete dehydration and then being able to withstand dry conditions and other environmental extremes for over 10 years!

Survival as adults is an adaptation shown by several aquatic groups. It is at its most obvious in winged groups, the insects and birds, in which adults simply fly away from desiccated, unfavourable habitats. The Banded Stilt, *Cladorhynchus leucocephalus*, is a wader characteristic of many temporary salt lakes but which leaves these when dry to seek refuge elsewhere. Several dragonfly species characteristic of temporary fresh waters exhibit an analogous (though perhaps more complex) pattern of behaviour.

For adults unable to escape desiccation by flight, adaptation must of course take other more direct forms. In *Coxiella striata*, a gastropod of many mildly saline lakes in Australia, adult survival simply involves closure of the shell by tight adhesion of the operculum. In *Haloniscus searlei*, an isopod found in similar localities to *C. striata*, adult survival seems to be in favourable refuges such as under stones. Of animals found in temporary fresh waters and surviving the dry phase as adults, frogs provide some particularly interesting and clear examples. The development of more or less impermeable cocoons, of subcutaneous lymph sacs and enlarged bladders for water storage and of a physiology able to withstand significant water loss are amongst the more obvious adaptations displayed by adults of several species of *Cyclorana*, *Neobatrachus* and *Limnodynastes* to the ephemerality of waters in the arid regions of Australia (Williams 1985).

Many of the adaptations considered above are simply specific adaptations within a suite of life-cycle adaptations which has evolved as part of an integrated strategy for survival in ephemeral waters. Adaptations required within the suite usually include rapid growth rates, the ability to synchronize life-cycles with the occurrence of water and good dispersal mechanisms. Overall, in fact, the suite of adaptations required corresponds to those usually regarded as characteristic of so-called *r*-selected or "opportunistic" species.

Within such species living in temporary waters, however, four major lifecycle strategies may be discerned according to the balance struck between adaptations, especially those adaptations ensuring survival during the dry phase and dispersal (see Fig. 8.3). Good examples of all four types of lifecycle strategy are found amongst Australian aquatic animals.

In the first of the strategies, type a, the species involved lie dormant during the dry season and do not actively disperse from the locality inhabited. Most of the invertebrates of Australian salt lakes have strategies of this type. In the second strategy, type b, the species also lie dormant during the dry season, but some active dispersal takes place. Most of the insects of Australian temporary water-bodies have strategies of this type. In the third sort of strategy, type c, there is no dormant stage, but there is active dispersal enabling use of permanent water when temporary waters are dry. And, in the final strategy, type d, there is again no dormant stage. Active dispersal involves the use of temporary waters only. Only insects and birds have strategies of types c and d.

In three strategies, b-d, an efficient dispersal mechanism clearly is an important or critical adaptation. Winged flight provides this mechanism for almost all the animals involved. Thus, whilst insect and avian flight did not evolve in response to habitat ephemerality, the ability to fly, once evolved, gave its possessors a powerful new vehicle for expansion into new niches, namely ephemeral waters. Efficient dispersal mechanisms also are important for species with life cycle strategies of type a and which live in unpredictably filled waters, i.e. those not filled annually, such as Lake Eyre. The rapid colonization of such waters by animals other than insects and birds can only be by passive dispersal in flood

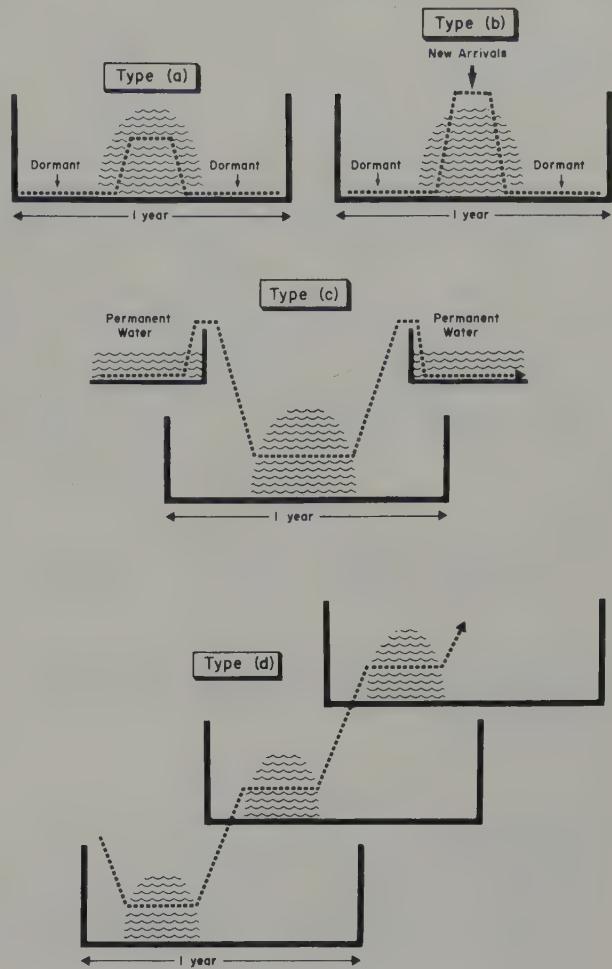


Figure 8.3 Life cycle strategies of animals in ephemeral water-bodies. (After Williams, 1985) [R. Evans]

waters, by wind, or through some other agency. So far as the fauna of predictably filled temporary waters is concerned, however, the need for efficient dispersal mechanisms may have been over-estimated by previous authors. Perhaps the best "game plan" for these animals is to remain *in situ* and not risk transportation to a possibly unfavourable habitat. Perhaps the hook-like protuberances on the ephippium of certain species of *Daphniopsis* are less a means of increasing the chances of transport from a lake on the feet of birds than a means of more firmly attaching the ephippium to the lake substratum and, thus, of decreasing the chances of transport.

The concept that at least certain animals may be served best by remaining *in situ* within a locality that has already proved to be favourable when containing water is in accord with the view that many temporary bodies of water are often environments with many advantages for those inhabitants who have evolved appropriate strategies to cope with the ephemeral presence of water. Amongst such advantages may be mentioned a relative freedom from competitors and predators and an abundance of food. This freedom from competition, Bayly (1978) suggests, has induced an increased degree of sexual dimorphism amongst calanoid copepods of temporary waters in Australia. This adaptation allows for greater efficiency in food exploitation in that a wider size range of food particles can be ingested. In similar vein, the rapid growth of *Paraborniella tonnoiri*, a chironomid whose larvae live in temporary fresh waters in Western Australia, is seen by Jones (1974) as an adaptation which capitalizes on the abundance of food as

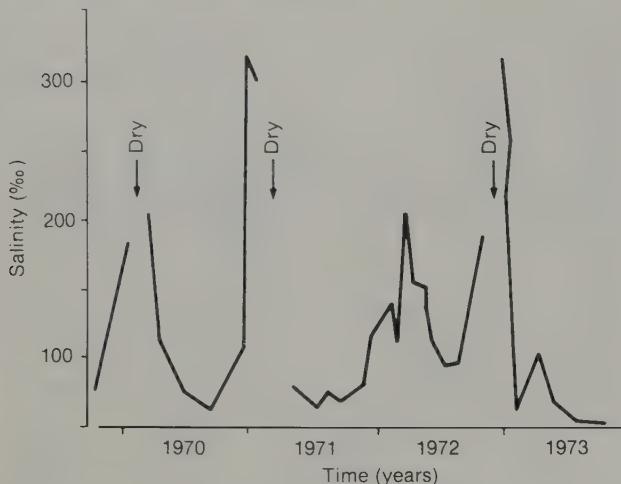


Figure 8.4 Salinity in Lake Eurack, Victoria, over a four year period. (After Williams & Buckney, 1976) [R. Evans]

a means of escaping certain predators, notably, another chironomid, *Allotrissocladius* sp. (it grows rapidly to a size too big to be eaten).

Adaptations to High Salinity

Many of the ephemeral waters mentioned in the previous section are saline, so that both unpredictably and predictably filled salt lakes are common and widespread aquatic habitats in Australia. As well, there are many salt lakes which permanently contain water. For the most part, the predictably filled temporary salt lakes occur in southwestern and southeastern Australia and most permanent salt lakes in western Victoria. Unpredictably filled temporary salt lakes are spread over a very large area of central Australia, but by no means uniformly.

Whilst the salinity of most of the permanent salt lakes remains relatively stable (though often at a high value, e.g. 70‰ in Lake Gnotuk in Victoria), the salinity of temporary salt lakes may range annually from values below 50‰ to values in excess of 300‰. Figure 8.4 illustrates the extent of variation in salinity that occurred in Lake Eurack in Victoria over a four year period.

Animals that live in saline lakes, therefore, not only must have adaptations to cope with high environmental salinities, but also must have the ability to cope with wide salinity

Table 8.2 Salinity maxima at which some important halobionts of Australian salt lakes have been recorded in the field. (Data after various sources)

TAXON	SALINITY (‰)
Anostraca: <i>Parartemia zietziana</i>	353
Ostracoda: <i>Diacypris whitei</i>	180
Copepoda: <i>Calamoecia salina</i>	131
Isopoda: <i>Haloniscus searlei</i>	192
Mollusca: <i>Coxiella striata</i>	112
Insecta: <i>Tanytarsus barbitarsis</i>	95
Pisces: <i>Taeniomembras microstomum</i>	70

fluctuations. Additionally, but not to any significant degree in Australia, variation in the relative proportions of the ions involved may perhaps provide a further chemical stress for animals found in salt lakes.

On a global basis, the number of animal species that has adapted to high and fluctuating salinities in inland waters is relatively few (vis-à-vis numbers in fresh waters). And, as a general rule, but no more than that, the higher the salinity of a given water-body, the fewer the species present. This relative paucity of salt-adapted species and the general correlation of species number and salinity also apply within Australia. There are several features, however, which distinguish the fauna of Australian salt lakes from that elsewhere. The documentation of some of these is of interest.

First, there are some indications that within some groups diversity is higher in Australia than elsewhere. Diversity is high, for example, in the halotolerant ostracods of Australia and amongst the Australian brine shrimp genus *Parartemia*. Similar diversity does not apply in these groups on other continents. Second, almost all of the species present in Australian salt lakes are endemic. Third, forms often common in salt lakes outside Australia are either absent or rare in Australian salt lakes. *Artemia* and ephydriids provide examples. And, fourth, some elements of the Australian salt lake fauna are unique; *Haloniscus searlei* and *Coxiella* are, respectively, the only oniscoids unequivocally known to have adapted to life in salt lakes and the most halotolerant of all known gastropods. Reference to Chapter 7 will indicate that these features closely reflect the more generally applicable differences of the fauna of Australian inland waters from aquatic faunas on other continents.

Taken overall, the features also point to the comparative success achieved by the fauna in adapting to another of the salient features of Australian inland waters, namely high salinity. Indeed, it is interesting to record that several species found in Australian salt lakes are amongst the most tolerant of halobionts known. Table 8.2 lists the maximum salinities at which some of the more common inhabitants of Australian salt lakes have been recorded in the field. Most of the salinities exceed 100 g L⁻¹, a value well in excess of that tolerated by most species in salt lakes outside Australia.

Despite the great tolerance of certain animals living in salt lakes, there are, nevertheless, not many animals, either in Australia or elsewhere, which have developed adaptations to cope with very high salinities. Most salt lake animals cannot tolerate salinities of more than about 50 g L⁻¹. This paucity of salt-adapted species provides a basis for dividing the fauna of Australian salt lakes into three general categories: (1) halobionts, i.e. those animals adapted to salinities >50 g L⁻¹, e.g., *Parartemia zietziana*, *Calamoecia salina*; (2) halophiles, i.e. those animals adapted to salinities between about 10 and 60 g L⁻¹, e.g., *Daphniopsis* spp., *Coxiella striata*; and (3) salt tolerant freshwater species, i.e. those animals found in lakes with salinities below about 20 g L⁻¹.

As for the actual mechanism by which halotolerance is achieved (the nature of the adaptation), the most important clearly concerns physiological effects in internal body and cellular fluids. The two basic phenomena involved are conformity and regulation. In the former case, either body fluid and/or cellular fluids conform osmotically (or ionically) with fluids outside the body or cell. In the latter case, physiological mechanisms enable the animal actively to regulate the osmotic strength (or ionic proportions) of its internal fluids. Examples of osmoconformers, at least so far as body fluids are concerned, are the calanoid species *Calamoecia salina* and *C. clitellata*. *Haloniscus searlei* and *Parartemia zietziana* are examples of osmoregulators. *Coxiella striata* is an example which osmoregulates body fluids over part of the salinity range and osmoconforms at high salinities.

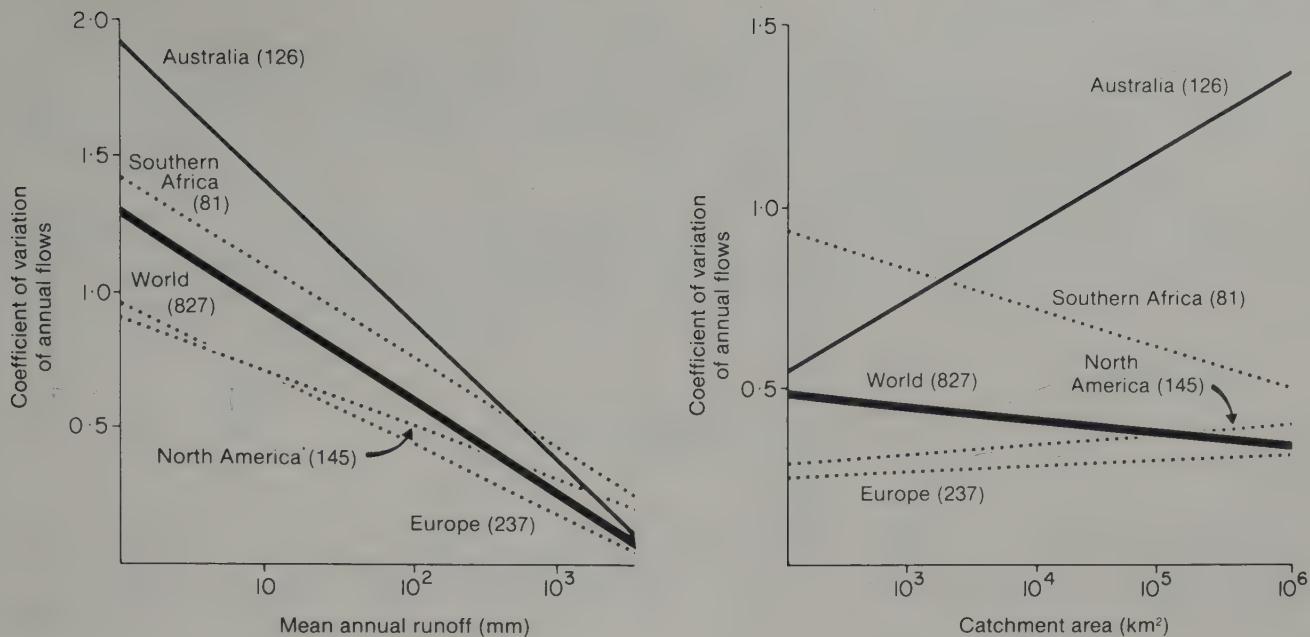


Figure 8.5 Coefficient of variation of annual flows in 827 rivers (= "large streams") versus mean annual runoff and catchment area. (After McMahon, in press)

[R. Evans]

Many adaptations are needed for survival in highly saline environments, not all directly concerned with the physiological consequences of high and, perhaps, unfavourably proportioned amounts of dissolved salts in the external medium. None appears restricted to species of Australian waters and no discussion of them is attempted. Since salinity and the concentration of dissolved oxygen are closely correlated, some of the more important additional adaptations required relate to the low ambient concentrations of oxygen in salt lakes. In response to low ambient concentrations of oxygen, several Australian species in salt lakes have developed respiratory pigments, the ability to regulate rates of respiration and adaptive behavioural patterns.

Adaptations to Hydrological Changes in Flowing Waters

The highly variable discharge values characteristic of Australian flowing waters in both low and high rainfall areas of the continent were briefly mentioned in Chapter 7 and various comments on this matter have also been made earlier in this account *passim*. For purposes of discussion here, these previous comments may be summarized by the statement that over large areas of Australia the interplay of climatic variability and a generally flat topography means that many Australian rivers and streams exhibit marked seasonal and secular hydrological changes. Thus, during dry phases or the dry season, Australian streams and rivers may flow quietly within well-defined courses, consist only of a series of pools with little or no interconnecting surface flow or disappear altogether. During a wet phase or the wet season, on the other hand, these same streams or rivers may inundate vast areas of adjacent floodplain and their downstream flows may be exceedingly high. In short, marked hydrological fluxes are a salient feature of many flowing waters in Australia. Figure 8.5 succinctly summarizes this phenomenon and Fig. 8.6 illustrates the nature and extent of seasonal differences in streamflow for various important rivers in Australia.

The physical changes in the environment wrought by these hydrological changes take many forms. They are perhaps best illustrated by reference to particular examples. Thus, in

northern, monsoonal parts of Australia, rivers inundate extensive floodplains during the wet, summer season and have very high discharge values. During the dry, winter season, these same rivers usually dry to a series of river pools which may or may not be interconnected. The floodplain then contains only isolated water-bodies or is quite dry. Note that almost 40% of all the water discharged from the continent is carried by these so-called flood/drought northern rivers.

Different environmental effects result from the hydrological changes within the Murray River, another particular example. Here, maximum discharge takes place during the winter, the wet season in this part of Australia. Seasonal differences in flow are not as massive as in northern rivers, but, even so, extensive floodplain inundation and the filling of billabongs and wetlands associated with (and often originating from) the river are natural events in the wet season. During the dry, summer season, many of the wetlands dry, the billabongs become isolated from the river and the river itself has greatly decreased flows. To a considerable degree, the artificial impoundment of this river has altered the natural flow regimen (Walker, 1985; 1986).

Coastal rivers and streams in southeastern Australia provide a third example of flowing waters of interest in the present connection. Many of these flow strongly in the winter wet season, though often without extensive flooding of adjacent areas, but during the summer dry season they contract to a series of large river pools with only small amounts of interconnecting flow. Again, the hydrological regimes of many of these rivers have been changed by man.

As for the adaptations to marked hydrological changes in Australian rivers and streams, it must first be said that although some adaptations are clear and can be discussed, not a great deal of information on this subject is available. This is surprising given the obvious nature of hydrological change within the Australian limnological scene; it is also disturbing given recent attempts by several water resource authorities to take more into consideration than in the past on environmental consequences of river regulation (*i.e.* there is not a lot of information upon which to base sensible river management).

8. AQUATIC FAUNA ORIGINS

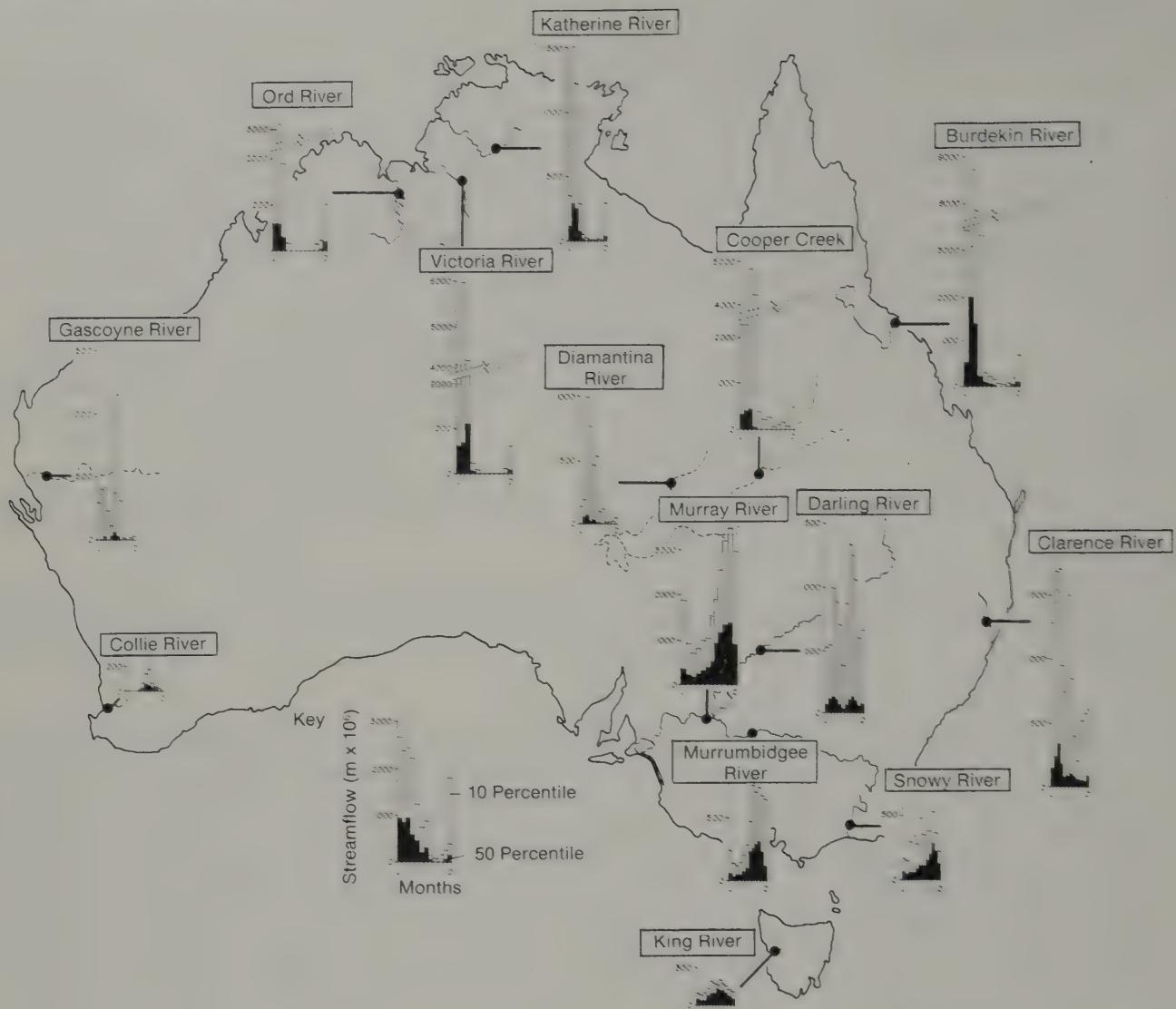


Figure 8.6 Variability of monthly streamflow for selected rivers throughout Australia. The graphs show monthly streamflow values likely to be equalled or exceeded one year in 10 or one year in two. Note different scales of vertical axes. (After Department of National Resources, Australian Water Resources Council, 1978)

[R. Evans]

The clearest examples of adaptation to marked hydrological fluctuations involve life cycle events and good illustrations are provided by various fish and waterbird species and at least a few invertebrate species. Several species of fish have breeding periods synchronized with the hydrological regime such that spawning occurs only after a rise in river levels (Cadwallader, 1986). Breeding follows flooding. The adaptive advantages of this are manifold, but one in particular is obvious: the young fish develop at a time when nutrients released from recently flooded sediments stimulate the growth of food organisms either directly or through the food chain. The golden and silver perch found in the Murray River are two species whose breeding cycles follow this pattern. For them, flooding is an obligatory prerequisite for breeding. In several other fish species, e.g. the Murray Cod, breeding also occurs at flood times, but it appears then more a matter of seizing an opportunistic advantage than of obligatory correlation. Fish which require floodwaters to breed resorb eggs if flooding does not eventuate.

The type and number of fish eggs produced are related features which seem to be adaptively correlated with flow requirements in a more general fashion. Thus, whilst most freshwater fish do not produce numerous and floating eggs, the Golden Perch does, and perhaps this helps in the wide dispersal of the species in floodwaters.

Breeding adaptations to hydrological changes are shown, too, by many aquatic birds, especially several duck species characteristically associated with riverine wetlands in southeastern Australia. The Black Duck and the Grey Teal provide examples. The breeding pattern in such species is for reproduction to commence when water levels begin to rise. If unsuitable environmental conditions develop, then adults simply fly to more favourable habitats. Breeding cycles, therefore, are opportunistic in the sense of being correlated with flooding irrespective of where and, also to some degree, when this occurs. This pattern of breeding and dispersal contrasts strongly with that shown by most Northern Hemisphere species of waterfowl. For these, the pattern involves precisely timed migrations in predictable directions with breeding closely controlled by changing day-length and temperature.

Australian waterfowl, by contrast, have imprecisely timed migrations in unpredictable directions with breeding dependent upon the occurrence of favourable habitats. Obviously, the patterns displayed by Australian species are of much greater adaptive value in an environment where marked hydrological fluctuations occur.

As a final example of an adaptation to the marked hydrological fluctuations of many Australian flowing waters, brief reference is made to the breeding cycle of *Paratya australiensis*, an atyid prawn which typically occurs in lowland streams and rivers in southeastern Australia. Unlike most

freshwater invertebrates, this species produces planktonic larvae. Normally such larvae would be swept downstream in the current. In the case of *P. australiensis*, however, breeding is in synchrony with the seasonal changes in streamflow; breeding commences in summer shortly before the inhabited rivers and streams dry to a series of pools within which flow is negligible. By the time of larval release, the pools have developed and provide a suitable larval habitat. Larval growth is rapid and the young prawns are able to resist being washed downstream by the time the rivers and streams are once more flowing strongly.

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8. AQUATIC FAUNA ORIGINS

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9. THE DISCOVERY OF THE AUSTRALIAN FAUNA AND THE ESTABLISHMENT OF COLLECTIONS

P. J. STANBURY

Kangaroo, Kangaroo!
Thou Spirit of Australia,
Be still the glory of this land
Happiest Work of finest Hand!

From the first volume of poems published
in Australia; Baron Field, 1814

INTRODUCTION

The fauna of Australia was discovered and rediscovered by a succession of people. Each group had a variety of purposes in mind. This caused them to look at the fauna in different ways. The Aborigines, for example, as well as regarding the fauna as food, understood that animals were, by and large, partners in the land. Abundance of the fauna depended on the seasons and on natural occurrences. The origin of species

and their character were explained by legends which were retold from generation to generation. Images of the fauna were recorded in paintings and rock engravings.

The first explorers were primarily adventurers and their contact with the fauna was mainly trivial. In September 1606, Luiz Vaez de Torres' companion, Diego de Prado, reported so many flies off the Queensland coast "that it seemed as if they wanted to eat the men up". His impression was confirmed by Francis Pelsaert (November 1629), William Dampier (January 1688), Nicolaus Witsen (October 1698) and by numerous others down to the present.

Later, professional collectors came. They carefully preserved specimens, taking notes and drawings for their patrons and fellow men of science in Europe. Among the best known collectors were Sir Joseph Banks on Cook's first voyage and the scientists on Nicolas Baudin's voyage and other French expeditions. In general, the early French zoological work on Australia's fauna was carried out much more consistently and competently than that by the English.

Deck hands regarded the fauna with a seamanlike attitude. Joseph Banks recorded a sailor's description of a flying fox "about as large and much like a gallon keg, as black as the devil and had two horns on its head". Such descriptions must have been similar to those of the first European settlers.

The new wave of people that arrived in 1788 were mostly ill-educated and interested only in survival and thoughts of home on the other side of the globe. The local fauna was sometimes considered as food, but also as vermin and a source of fun or sport. By and large, it was unfamiliar and, therefore, compared unfavourably with the familiar animals at "home", especially by those that came from the soft English countryside in which the familiar animals of childhood had left a lasting impression.

Nevertheless, publications with sections about the Australian fauna began to appear. By 1805, specialized accounts of the insects had been published, including Donovan's *Insects of New Holland* and Lewin's *Prodromus Entomology*.

As the settlement came of age, some local people with property started to take an interest in natural curiosities. In 1821, a Philosophical Society was started. Two of its aims were to found a library and a museum.

Some immigrants brought collections with them (Fig. 9.1). Alexander Macleay, who arrived in 1826, imported a notable entomological collection resulting from at least twenty-five years of acquisition, exchange and purchase. Macleay was

Figure 9.1 Alexander Macleay came to Australia in 1826 bringing with him important insects obtained by purchase and exchange from many notable collections in England and Europe. Macleay was responsible, at least in part, for the setting up of Australia's first public museum, the Australian Museum in Sydney; other members of the family were later associated with it as Trustees. (From an engraving of a painting by Sir Thomas Lawrence, for the Linnean Society of London)



Figure 9.2 Naturalistic Aboriginal cave paintings, painted perhaps 20,000 years before the present in Arnhem Land. The freshwater crocodile (*Crocodylus johnstoni*) is 3,370 mm long; wallabies, other animals and hand prints can also be seen. (From Chaloupka, 1984, with permission)

responsible in large part for the establishment of the first public museum in Australia, the Australian Museum, at first called the Colonial Museum. There is some controversy over the date that the Museum came into existence, but the 150th anniversary was celebrated in 1977.

Other States also founded museums as soon as those in power could be persuaded to make a contribution from the public purse: Hobart, Melbourne, Adelaide and Brisbane all had public collections by 1862.

The stimulus for the foundation of the museums was in part due to visits, sojourns and residence of men of science, to the export of specimens to overseas museums, to the enthusiastic discovery of colourful birds, unique mammals, reptiles and fishes and to associated discoveries in the fields of botany and geology. The latter were of particular importance to a young colony struggling economically.

The discoveries came about as the result of explorations and expeditions, both by sea and land. The sea voyages were more or less extensions of those that led to the discovery of the continent itself. The inland treks were arduous and today seem extraordinary achievements to travellers in a modern vehicle or with lightweight hiking gear. The wonder is that specimens were collected at all or notebooks kept.

This Chapter summarizes the discovery of Australia's animals and traces the efforts of some of the personalities who worked to establish public collections of fauna prior to World War II.

THE FAUNA DISCOVERED BY ABORIGINES

Geological, archaeological and anthropological evidence suggests that Aboriginal people first colonized Australia about 50,000 years ago (ybp). The Aborigines, like the rest of mankind until only about 10,000 ybp, lived by hunting and gathering food. In consequence, they observed animals very closely. Their observations were passed on by personal teaching from generation to generation and recorded in paintings. Aborigines are believed to have painted or engraved the rocks of their various territories for at least 35,000 years.

Chaloupka (1984) published a chronology of the Arnhem Land Plateau rock art. The earliest form of expression, hand prints, give way to naturalistic animals about 20,000 ybp. These animals are drawn confidently (Fig. 9.2) and consist of a filled outline. Details characteristic of species often are emphasized. Table 9.1 lists some of the species depicted; some species now extinct in the area were obviously alive and well 20,000 ybp.

9. DISCOVERY AND COLLECTIONS

Table 9.1 Animals depicted by Aborigines of the Arnhem Land Plateau 18,000–20,000 ybp. (Information from Chaloupka, 1984)

COMMON NAME	SCIENTIFIC NAME
LIVING SPECIES:	
Antilopine Wallaroo	<i>Macropus antilopinus</i>
Northern Black Wallaroo	<i>Macropus bernardus</i>
Alligator River Euro	<i>Macropus robustus</i>
Agile Wallaby	<i>Macropus agilis</i>
Rock Possum	<i>Pseudochirus dahli</i>
Bandicoot	<i>Perameles sp.</i>
Echidna	<i>Tachyglossus aculeatus</i>
Rock Python	<i>Morelia oenpelliensis</i>
Freshwater Crocodile	<i>Crocodylus johnstoni</i>
EXTINCT SPECIES:	
Thylacine	<i>Thylacinus cynocephalus</i>
Numbat	<i>Myrmecobius fasciatus</i>
Tasmanian Devil	<i>Sarcophilus harrisii</i>
Long beaked Echidna	<i>Zaglossus</i>
Marsupial Lion	<i>Thylacoleo</i>
Marsupial Tapir	<i>Palorchestes</i>

Table 9.2 Animals depicted by Aborigines in cave paintings in the Cober Pediplain. (Data extracted from McCarthy, 1976)

TAXON	NUMBER OF EXAMPLES
MAMMALS:	
kangaroo	127
dingo	9
bandicoot	33
marsupial rat	1
kangaroo rat	2
phalanger	2
possum	3
echidna	4
horse	5
koala	1
unidentified	17
BIRDS:	
emu	113
mallee hen	3
cockatoo	1
goose	3
unidentified	16
REPTILES:	
snake	22
goanna	9
stumpy tail	7
dragon	5
skink	5
tortoise	7
AMPHIBIANS:	
frog	4
FISH:	
	10
INVERTEBRATES:	
crayfish	1
insect	3

The naturalistic depictions give way to a more dynamic form around 18,000 ybp. These images include macropodids such as the Northern Black Wallaroo, *Macropus bernardus*, the Emu, *Dromaius novaehollandiae*, the Echidna *Tachyglossus aculeatus*, the Rock Ringtail Possum, *Pseudocheirus dahli*, a rock python, *Morelia oenpelliensis*, several birds and a freshwater fish. Some of the paintings, which often are associated with human male hunters, show the tracks of the animals. From the mouth may emanate dashes or other markings which are thought to represent blood or cries, perhaps the first recordings of animal vocalization (Fig. 9.3).

Around 7,000 ybp, the sea level rose and different animals appear in the paintings for the first time, having been newly introduced by the new estuaries and rivers. Barramundi (*Lates calcarifer*) became an important item of diet for the local tribes and it was commonly depicted. Less frequent paintings include mullet (*Liza diadema*), catfish (*Hexanematichthys leptaspis*), flying foxes (*Pteropus alecto*) and the Saltwater Crocodile (*Crocodylus porosus*), but all images revert to a naturalistic rather than the dynamic stylised form prevalent before the rivers rose. Interestingly, representations of the boomerang decrease while new forms of spear appear, together with spear throwers.

The Thylacine (*Thylacinus cynocephalus*) and Emu (*Dromaius novaehollandiae*) rarely are depicted and presumably moved inland. *Thylacinus* eventually became extinct on the mainland.

From around 6,000 ybp, X-ray paintings were made showing the shape of the internal organs and position of the bones.

Investigation of shell middens of this period shows the appearance of freshwater mussels (*Velesunio*). These animals also are depicted in paintings.

Chaloupka's discussion of the Aboriginal paintings of Arnhem Land include comments on the legendary dreamtime heroes, half man and half beast and on the Lightning Man, Namarrgon. The latter appears in the painting galleries at about the geological time of prolonged wet season (and presumably lightning).

The northern and drier parts of Australia are rich in galleries of Aboriginal paintings. Several factors contribute to this top-heavy distribution: (i) suitable climate for preservation of paintings, (ii) relatively little disturbance by Europeans and (iii) the presence of suitable rock shelters and painting materials.

Other examples of studies made of Aboriginal galleries include those of Trezise (1971), southeastern Cape York; Brandl (1973), western and central Arnhem Land; and McCarthy (1976), central western New South Wales. All show a variety of paintings representing fauna. Most authors are reticent about ascribing specific age, preferring to categorise the overlapping layers of paintings by style or terms such as old, early and late. Brandl (1973) for example, states that paintings of the Thylacine in Arnhem Land are associated with Mimi art, whereas dingoes occur in X-ray art and other recent styles.

The exact dating is less important than the fact that there is a chronology and, whatever the first European explorers felt, the Aboriginal people observed, drew, dissected and studied Australia's animals and studied their ecology before any white man (Table 9.2).

Rock engravings confirm Aboriginal interest in the fauna. The sandstone around Sydney proved particularly suitable for engravings; there are thousands of sites in the region. Most of them include animals such as macropodids, whales, fishes and birds (Cambell, 1898). One site near Wiseman's Ferry has particularly fine engravings, including one of an Emu standing over a clutch of eleven eggs (Fig. 9.4). The site is to

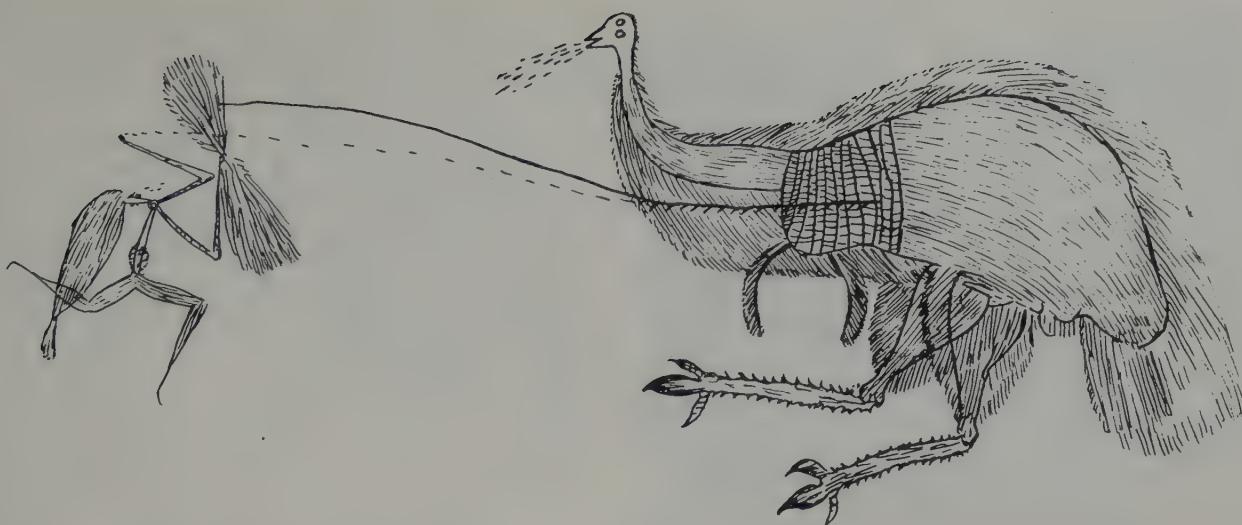


Figure 9.3 Drawing from the period of dynamic Aboriginal cave paintings 17,000 years before the present. A hunter is shown spearing an emu; dashes from the man's mouth are thought to represent a cry of success; those from the emu's beak may be either blood or a death rattle; while other dashes show the path of the spear. (From Chaloupka, 1984)

be developed as an interpretation centre (Stanbury & Myers, 1983) and, hopefully, this will lead to research in dating engravings. The very ease with which engravings can be made indicates that weathering may occur readily. The average engraving in the Sydney region seems unlikely have a life of more than a thousand or even several hundred years unless it was re-engraved from time to time.

Rock engravings add to the list of species for which we have indisputable evidence of Aboriginal discovery in relatively recent time, but paintings may provide a better record of the more distant past.

Another recent proof of the range of animals known by Aborigines is the sign language handed down from generation to generation by tribes living in north Queensland (Fig. 9.5) (Roth, 1908).

FIRST EUROPEAN SIGHTINGS

With the benefit of hindsight, to pluck from the mass of medieval writings those phrases which point to the existence of an unexpected and fabulous Antipodean land is relatively easy. No map was convincing, however, until Claudius Ptolemy's manual on how to draw maps, originally written about A.D. 160, was rediscovered at the end of the 14th Century. When the information was circulated widely by the newly invented printing press, a "Ptolemy map" appeared in 1475 which showed a southern Terra Incognita. This land linked southern Africa to the west of India.

During the following century, Portuguese and Spanish sailors rounded the Cape of Good Hope, discovered America and sailed through the waters that separate New Guinea and Australia. By 1536, much of the northern coastline of Australia had been charted. Parts of the eastern coastline had been seen, although some of the voyages and discoveries were kept secret to avoid political trespass.

Chinese landings possibly took place in northern Australia, but indisputable evidence does not exist.

Mention has been made already of Luis Vaez de Torres' irritation with Australian flies in 1606. In 1611, Dutchman Hendrik Brouwer pioneered a new route to the Indies. This involved sailing eastward from the Cape of Good Hope to near the coast of Western Australia and then turning north.

The prevailing winds made this route faster than going north up the coast of Africa. The new route also meant that unexpected landings were made on the western coast of Australia, which consequently became known as New Holland. The discovery of the land fauna by Europeans began.

One of the early notable reports was the first written account of a small kangaroo, *Macropus eugenii*. The author, Dutchman Francis Pelsaert, wrecked in the *Batavia* off the West Australian coast, also described termite mounds, birds, three kinds of fish and multitudes of flies. Of the kangaroo he noted "below the belly the female carries a pouch ... inside this pouch are her nipples ... We have seen some young ones lying there". He guessed wrongly that the young grew from the nipples.

The Black Swan (*Cygnus atratus*) was first described on 5 July 1636 by Antonie Caen, captain of the Dutch ship *Banda*, again off Western Australia, as a large stately bird, half a yard long with an orange yellow bill.

Yet another Dutchman, Abel Janszoon Tasman on a voyage of unfulfilled promise, in December 1642 described Tasmania. His men saw the footprints of a clawed dog-like animal, probably those of a Thylacine.

Forty-six years later in 1688, the English pirate William Dampier saw more canine-like footprints in the Kimberley district of Western Australia. If these were made by a Dingo (*Canis familiaris dingo*), then priority must be given to the Dutchman Carstenzoon, who in May 1623 also saw similar footprints inland from the Gulf of Carpentaria. The first European sighting of a live Dingo appears to be that of Willem de Vlamingh's crew who saw a "yellow" dog when exploring near the present site of Perth in 1697.

Vlamingh's expedition is noteworthy because collections were made. Three black swans were taken alive. They survived the journey to Batavia, but died before they could be taken to Holland. A box containing shells reached Amsterdam in 1698, perhaps the first Australian natural history specimens to reach Europe. Vlamingh, like Dampier, also saw the Dugong (*Dugong dugon*) (Heeres, 1899).

When Dampier made a second voyage in 1699, he made some drawings of Australian birds, the first published field drawings made in New Holland. They appeared in 1703 in his *Voyage to New Holland* (Figs 9.6 & 9.8). Dampier was



Figure 9.4 Aboriginal rock engraving of an emu and eggs, together with footprints. This engraving is at a site near Sydney.

[P.J. Stanbury]



Figure 9.5 Aboriginal sign language identifying animals in Northern Queensland was handed down from generation to generation. Key: 1. Large kangaroo; 2. Large kangaroo; 3. Male red kangaroo; 4. Female red kangaroo; 5. Kangaroo in general; 6. Female brown kangaroo; 7. Male brown kangaroo; 8. Kangaroo in general; 9. Scrub wallaby; 10. Small rock wallaby; 11. White wallaby; 12. Possum; 13. Paddymelon; 14. Native companion; 15. Possum; 16. Pelican; 17. Echidna; 18. Bandicoot; 19. Native companion; 20. Echidna; 21. Duck; 22. Cockatoo; 23. Bee, honey; 24. Emu. (From Roth, 1908)

also the first European to describe an Australian reptile, the Shingleback, *Trachydosaurus rugosus*. His description shows remarkable observation for a non-biologist and includes the results of a crude dissection.

"And a Sort of Guano's, of the same Shape and Size with other Gauno's describ'd but differing from them in 3 remarkable Particulars: For these had a larger and uglier Head, and had no Tail: And at the Rump, instead of the Tail there, they had a Stump of a Tail, which appear'd like another Head; but not really such, being without Mouth or Eyes: yet this Creature seem'd by reckon'd a fourth Difference, the Legs also seem'd all 4 of them to be Forelegs, being all alike in Shape and Length, and seeming by the joints and Bending to be made as if they were to go indifferently either Head or Tail foremost. They were speckled black and yellow like Toads, and had Scales or Knobs on their Backs like those of Crocodiles, plated on to the Skin, or stuck into it, as part of the Skin. They are very slow in Motion; and when a Man comes nigh them they will stand still and hiss, not endeavouring to get away. Their Livers are also spotted black and yellow: And the Body when opened hath a very unsavoury Smell. I did never see such ugly Creatures any where but here. The Guano's I have observ'd to be very good Meat: And I have often eaten of them with Pleasure; but tho' I have eaten of Snakes, Crocodiles and Allegators, and many Creatures that look frightfully enough, and there are but few I should have been afraid to eat of; if prest by Hunger, yet I think my Stomach would scarce have serv'd to venture upon these N. Holland Guano's, both the Looks and the Smell of them being so offensive."

Table 9.3 lists some of Dampier's sightings. He collected both plants and animals; unfortunately only the plants seem to be in existence today (Whitley, 1970).

Well into the 18th Century, the relation between the Australian mainland, Tasmania and New Zealand was not clear. Some people believed that New Zealand was part of Antarctica or was part of a large Southern Continent distinct from "New Holland". Nevertheless, Australia was becoming a familiar concept to be viewed in a favourable light as the remarks added to a map published in 1744 show:

"it is impossible to conceive a Country that promises fairer from its Situation, than that of Terra Australis; no longer incognita... It lies precisely in the richest Climates of the world ... whoever perfectly discovers and settles it will become infallibly possessed of Territories as Rich, as fruitful, and as capable of Improvement, as any..." (Brown, 1744).

Such feelings and a general discontent with the over-sophisticated societies of Europe led to a further quickening of interest into the land of the wild, simple and noble savage. Thus, the scene was set for James Cook and his naturalists (Fig. 9.7).

THE FIRST SCIENTIFIC COLLECTORS

It was one of those occasions when the time was right. The intelligentsia of Europe were fired with enthusiasm for knowledge about the natural world and the Royal Society persuaded the Admiralty to send a ship to Tahiti to observe the passage of Venus. This provided an excellent opportunity of ascertaining the presence or absence of any great southern continent and of charting the extent of New Zealand. The wealthy Joseph Banks, later President of the Royal Society, through his connections but at his own expense, secured passages for himself and a number of companions. They joined the official astronomer, Charles Green, and his assistant, John Reynolds.



Figure 9.6 Dampier's 1703 map of New Holland where he saw "rackoons", birds, lizards, snakes, fish and shells. (From Dampier, 1703)

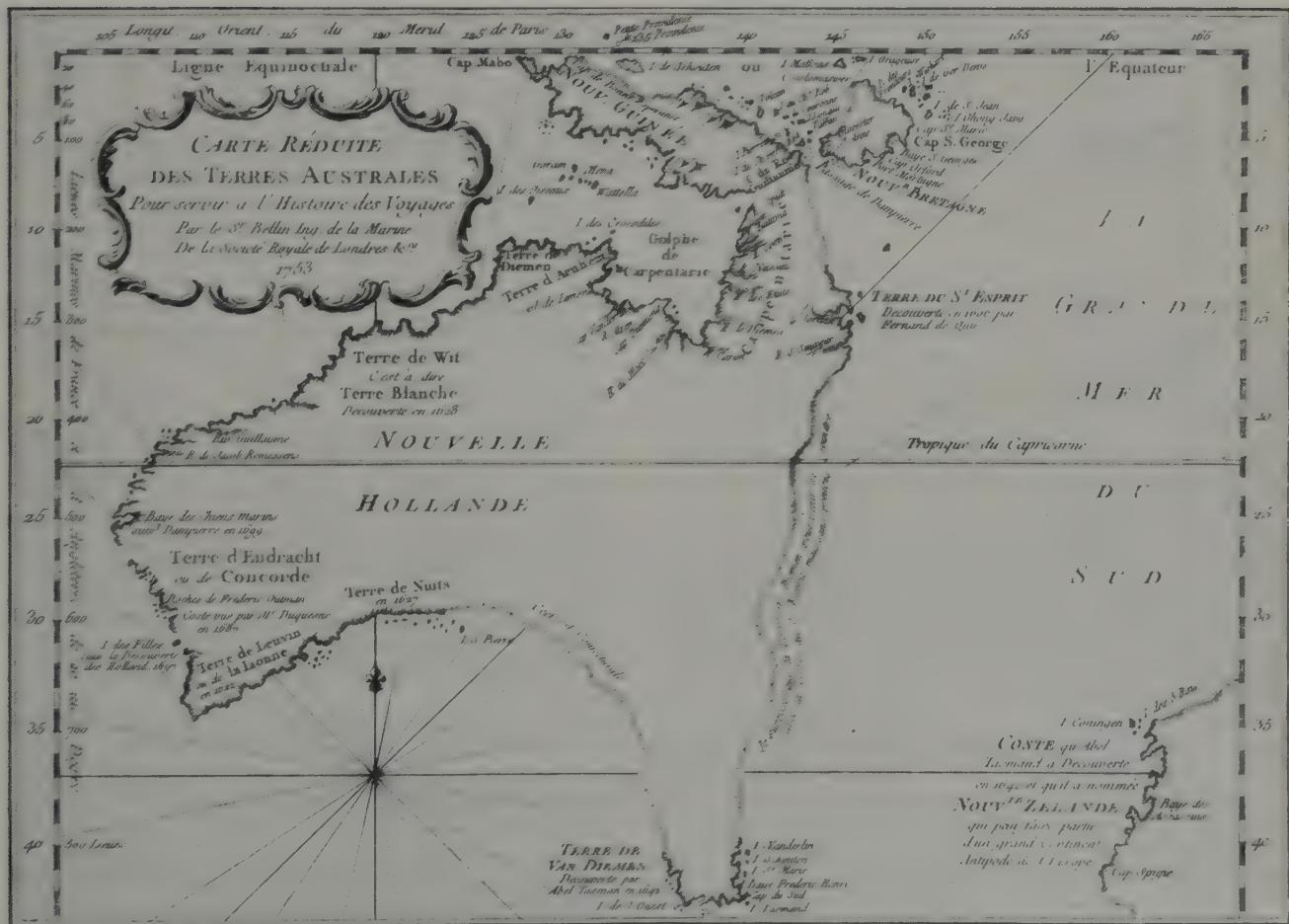


Figure 9.7 From 1650 to Cook's time, maps of Australia looked like this. Minor details (such as Dampier's Shark's Bay in Western Australia) were added from time to time, but it was Cook who put the coast of New Zealand and the eastern coast of Australia on the map.

9. DISCOVERY AND COLLECTIONS

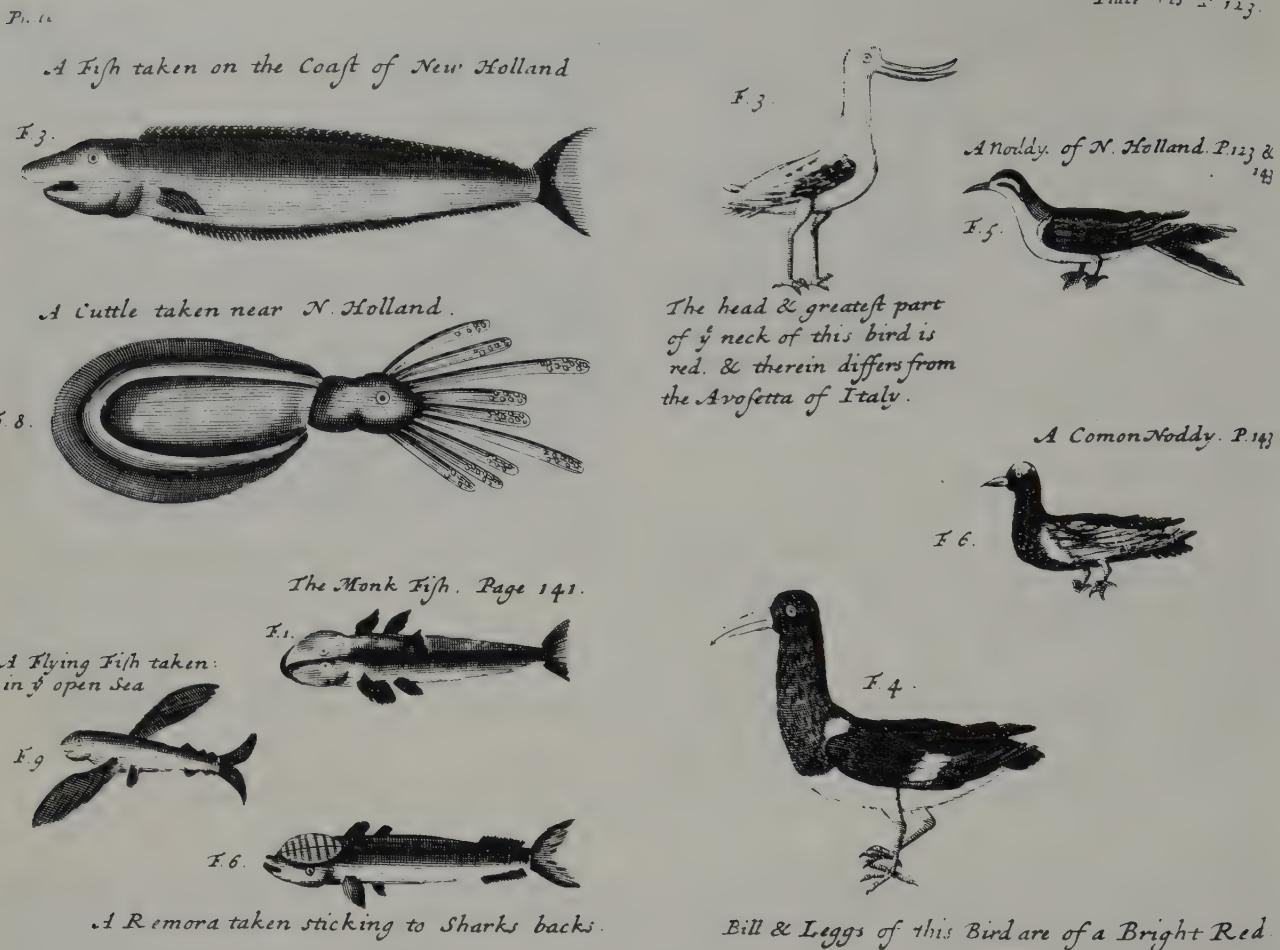


Figure 9.8 The first published figures of Australian fauna drawn from life were those of Dampier, made during his second voyage to Australia in 1699. They appeared in print in 1703 and include birds and fish. (From Dampier, 1703)

The choice of James Cook as captain was fortunate. After having spent six months exploring New Zealand, he decided that, although not specifically instructed to do so, charting the eastern coast of Australia would be worthwhile; and, incidentally, he claimed it for Britain.

Joseph Banks' choice of companions also was fortunate. Daniel Solander was a pupil of Linnaeus, which ensured that the species discovered would be named by the new scientific method which reduced the chance of confusion. An assistant naturalist from Sweden, Herman Sporing, was engaged, as were two artists, Sydney Parkinson and Arthur Buchan (who died at Tahiti, 1769), two white servants (James Roberts and Peter Briscoe) and two black servants (Thomas Richmond and George Dorlton), both of whom froze to death in Tierra del Fuego.

The men, their mental attitude and the evolutionary attic of the location all transpired to make the Cook and Banks visit an historic one. They spent over fifty days exploring and collecting on Australian soil; at Botany Bay (a week), Thirsty Bay and Endeavour River (where they repaired the ship after holing her on the Great Barrier Reef).

Cook thought the first landing place rather dreary "barren heath diversified with marshes and Morasses", but Banks and his party were so enthusiastic about what they found, Cook was persuaded to change his mind about naming the bay

after the stingrays they immediately saw on entering it. It became Botany Bay because of the excellent botanizing excursions.

Whitley (1970) compiled a list of the fauna they sighted, both in Australian waters and on the land excursions. He calculated that the scientists recorded over 500 different species compared to about the 100 known before Cook's voyage or the 24 recorded prior to Tasman's visit. His list, reproduced in Table 9.4, includes six marsupials: bandicoot, native cat, possum and three species of kangaroo. By way of comparison, thousands of species of plants were recorded from New Holland on the same voyage.

The drawings, paintings and notes made by Banks, Parkinson and others have survived in museums and libraries; many have been published. The whereabouts of the zoological specimens collected are much more difficult to establish. Most of them went to Banks' house in Soho, which was turned into a huge repository. From there some specimens were dispersed, some to museums, some to individuals for their cabinets which were eventually broken up and sold, perhaps to other collectors or museums, and some were borrowed for scientific work. The plant specimens received more care and a greater proportion was scientifically described.

Table 9.3 Some animals sighted by William Dampier and his crew in New Holland coastal waters during his second voyage in 1699.

MAMMALS:	REPTILES:
banded hare wallaby	land snakes
dingo	sea snakes
dugong	shingleback lizard
humpback whale	turtle
seal	
BIRDS:	FISH:
avocet	barracuda
booby	boneta
brindled tern	bream
cormorant	dogfish
crested tern	garfish
crow	leatherjacket
curlew	skate
duck	snapper
eagle	tiger shark
gannet	
gull	
hawk	
heron	
kite	
little corella	cockle
noddy	cuttlefish
pelican	fly
pied oyster catcher	limpet
turtle dove	mussel
INVERTEBRATES:	PERIODIC RECORDS:
	periwinkle
	oyster
	sea urchin
	termite

Whitehead (1969) summarized some of the formal exchanges in a detailed paper. Table 9.5 shows the fate of some groups. He concludes:

"The contrast between the care and attention paid to the botanical material from Cook's voyages, and the dispersal and neglect of the animal specimens, was principally due to Banks' mainly botanical leanings, Solander's early death and the perhaps deserved low standing of the British Museum at that time. Poor preservation techniques and the loss of information about specimens has resulted in nomenclatural problems of such complexity that zoologists have more than once regretted that the *Endeavour* was ever freed from the Great Barrier Reef. This is a limited view of the voyages. If the animal specimens have "softly and silently vanished away"; if Sir Joseph did eat just a few of them; if the kangaroo is now merely paint on canvas: what is this compared to the overall stimulus that Captain Cook's three historic voyages gave to natural history?"

Captain Cook's second visit to Australia, or rather to Tasmania, did not take place until 1770. His ships, the *Resolution* and the *Discovery* carried no naturalists, only the surgeon, William Anderson, and two artists, William Ellis, the surgeon's mate, and John Webber. The visit had little zoological significance.

The New Settlers and Their Observations of Fauna

Banks' house in Soho became a mecca for natural historians wanting to see specimens and Banks became the accepted authority on matters Australian. In 1779, he was asked to appear before a House of Commons Committee which was attempting to find a solution to overcrowding in Britain's gaols and their overflow, hulks of ships on the Thames.

Table 9.4 Some animals discovered on Cook's voyage to Australia in 1770. (Data extracted from Whitley, 1970, with taxonomy unchanged)

MAMMALS:
"Animal like a rabbit" [?bandicoot, <i>Perameles</i> sp.]
"Polecat or weasel" [= native cat, <i>Dasyurus quoll</i>]
porpoises, Family Delphinidae
grampus [perhaps the whale, <i>Megaptera australis</i>]
Captain Cook's kangaroo [<i>Wallabia canguro</i>]
flying fox [<i>Pteropus</i> sp.]
phalanger [<i>Pseudochirus peregrinus</i>]
large animal, 80lb [wallaroo, <i>Ozphranter reginae</i>]
smaller animals, 8.5lb [wallaby, <i>Macropus</i> sp.]
fer-de-cheval [horseshoe bat, genus indet.]
BIRDS:
Port Egmont hen
[= skua, <i>Catharacta skua lönbergi</i> , well out to sea]
albatrosses [<i>diomedea</i> sp., well out in Tasman Sea]
pintado bird
[= Cape pigeon, <i>Daption capense</i> , well out in Tasman Sea]
lorryquet [<i>Trichoglossus moluccanus</i>]
quail [<i>Coturnix pectoralis</i>]
<i>Nectris munda</i> [= allied shearwater, <i>Puffinus assimilis</i>]
bustard [<i>Eupodotis australis</i>]
black and white duck [could be pied goose, <i>Anseranas semipalmata</i> rather than burdekin duck, <i>Tadorna radjah rufitergum</i>]
egg bird [= sooty tern, <i>Sterna fuscata</i>]
<i>Nectris nugax</i> [= Audubon's petrel, <i>Puffinus l'herminier</i>]
pigeon [<i>Lopholaimus antarcticus</i>]
pigeon [= bar-shouldered dove <i>Geopelia humeralis</i>]
crow [= raven, <i>Corvus orris</i>]
goatsucker or churn owl [<i>Caprimulgus</i> sp.]
bee-eater [<i>Merops ornatus</i>]
a small bird with wattles
a bird like a tetrao [grouse-like bird, probably <i>Alectura lathami</i>]
owl [<i>Ninox</i> sp.]
white-breasted eagle of Lizard Island [<i>Haliaeetus leucogaster</i>]
oyster-cracker [<i>Haematopus unicolor</i>]
loxia of Parkinson [= tooth-billed cat bird <i>Scenopeocetes dentirostris</i> , fide H.J. de S. Disney pers. comm.]
black and white hawk [probably <i>Elanus scriptus</i>]
kite [<i>Milvus migrans</i>] [hawks, several species]
white cockadore [<i>Kakatoe galerita</i>]
brown cockadore [<i>Calyptorhynchus banksii</i>]
scaly-breasted loryquet [<i>Trichoglossus chlorolepidotus</i>]
doves [several species]
herns [several species]
whistling ducks [<i>Dendrocygna arcuata</i> and <i>Dendrocygna eytoni</i>]
shagg [any of 4 species of <i>Phalacrocorax</i>]
crane [probably brolga, <i>Grus rubicunda</i>]
ducks [including <i>Anas superciliosa</i>]
"Great Kingfisher of new Guinea" [<i>Kookaburra dacelo gigas</i>]
REPTILES:
loggerhead turtle [<i>Caretta caretta gigas</i>]
lizard of Lizard Island [? <i>Varanus semirex</i>]
water snake [<i>Boa pelagica</i> , = <i>Aipysurus</i> sp.]
FISHES:
sharks of Botany Bay including the whaler <i>Squalus vulpercula</i> [= <i>Galeolamna macrurus</i>]
leatherjackets [<i>Scobinichthya granulatus</i> or <i>Monacanthus macrolepis</i>]
stingray [= Captain Cook's stingray <i>Bathyoshia brevicaudata</i>]
stingray [<i>Urolophus testaceus</i>]
fiddler ray [<i>Trygonorrhina fasciata</i>]
shovelnose ray [<i>Aptychotrema banksii</i>]
whip ray [= eagle ray, <i>Myliobatis australis</i>]
mudskipper [<i>Euchoristopush kalolo</i>]
flying fish of N. Queensland [probably <i>Parexocoetus brachypterus</i>]
"flounders", indeterminable, also "flatfish"
fish from Endeavour River [<i>Drepanichthys punctatus</i>]
fish from Endeavour River [mango fish, <i>Eleutheronema tetradactylum</i>]
toadfish, etc from Endeavour River
epaulette shark [<i>Hemiscyllium ocellatum</i>]
large skate, or skate [perhaps <i>Urogymnus</i>] ... (cont.)

9. DISCOVERY AND COLLECTIONS

Table 9.4 Cont.

Raja radula [= rough ray, *Urogymnus asperrimus solanderi*]
skate or ray fish marked with polygons [perhaps *Himantura toshi*]
skate of an orbicular figure [probably *Taeniura lynima halgani*]
sharks, dogfish, rockfish, etc [indeterminable, some of the
identifications quoted by Beaglehole are not satisfactory]
mullet [*Mugil dobula*]
scomber of Parkinson or Cavalhi [= trevally, fam. Carangidae]
mackrel or mackerel [*Pneumatophorus australasicus*]
old wives [*Enoplosus armatus*, not in Dampier's sense of the term]
five fingers [morwong or jackass fish, *Nemadactylus macropterus*]

ASCIDIANS:

salps *Dagysa gemma* and *Dagysa cornuta* [= *Thalia democratica*]
salp *Dagysa strumosa* [= *Tethym vagina*]
sea squirt [probably *Cynthia praeputialis*]

INSECTS:

small butterfly between New Zealand and Australia
mosquito [*Aedes* and/or *Culex*]
green ant [*Oecophylla smaragdina virescens*]
"Caterpilar ... like wrathful militia" [larvae of limacodid moth]
cynips which fertilizes figs
termites [*Microcerotermes turneri*]
black ants in pith of tree [*Colobopsis* and *Tetraponera* spp]
butterflies over 3 or 4 acres [*Danais melissa hamata*]
pupa from which butterfly emerged [*Euploea sylvester*]
fly, culex of Parkinson [sandfly]
ants nesting in epiphyte plant
insects, miscellaneous. The insects of the *Endeavour* voyage were named
by Fabricius and a list of 221 species is given in A. Musgrave's
Bibliography of Australian Entomology, 1932 p. 86

CRUSTACEA:

megalopa larva of a crab, *Cancer erythroptalmus*
[= *Cancer cyapophthalmus*]
crab [*Portunus pelagicus*]
crab [*Portunus sanguinolentus*]
crab [*Matuta* sp. fide Whitehead, 1969, p. 177]
barnacles [*Lepas* or perhaps *Uperotis clava*]

OTHER ARTHROPODA:

scorpions, probably from Endeavour River district
centapees or centumpees [centipedes, probably from the Endeavour River
area]

ECHINODERMATA:

shell with rays or spikes [echinoderm]
sea eggs off Endeavour River [echinoderm]

MOLLUSCA:

violet snail, between Australia and New Zealand, [*Janthina janthina*
= *J. violacea*]
enormous cuttle [*Amplisepia verreauxi*]
Mimus volator [= sea lizard, *Glaucus lineatus*]
mud oyster [*Ostrea angasi* or *O. sinuata*]
rock oyster [*Saxostrea commercialis*]
mangrove oyster [*Crassostrea glomerata*]
large muscle [= mussel, *Modiolus* sp.]
pearl fishery envisaged
hammer oyster [*Malleus albus*]
Trochus perspectivus [= *Architectonica perspectiva*, the perspective sundial
shell]
large cockle, *Chama* [= giant clam, *Tridacna gigas*]
black hercules club [*Pyrazus ebeninus*]
[warrener, *Subninnella undulata*]
[Sydney turban shell, *Ninella torquata*]
coach road whelk [so-called in the Leverian Museum = cartrut shell,
Dicathais orbita]
ear shell [= abalone, *Notohaliotis ruber*]
spondylus [= thorny oyster, *Spondylus ducalis*]
top shell, *Trochus* [*Trochus niloticus*]
persian crown shell [= Baler Shell, *Melo diadema*]
turban shell [*Turbo undulatus*]
duck's bill patella [*Scutus*? or a limpet]
Sydney cockle [*Anadara trapezia*]
mussel [*Mytilus obscurus*]
hairy mussel [*Trichomya hirsuta*]
noddiwink [*Nodilittorina tuberculata*]
conniewink [*Bembicium melanostoma*]
bubble shell [*Bullaria botanica*]
australwink, [*Austrocochlea obtusa*]

Table 9.4 Cont.

Shells in Banks Collection which may have been collected
during the *Endeavour* voyage:

<i>Septifer bilocularis</i>	<i>Cypraea argus</i>
<i>Lithophaga teres</i>	<i>Cypraea talpa</i>
<i>Pinctada vulgaris</i>	<i>Cypraea arubica</i>
<i>Pinna muricata</i>	<i>Cypraea maculifera</i>
<i>Batissa triquetra</i> (or <i>B. violacea</i>)	<i>Cypraea histrio</i>
<i>Codakia tigerrina</i>	<i>Cypraea mauritiana</i>
<i>Corbis fimbriata</i>	<i>Cypraea tigris</i>
<i>Lioconcha castrensis</i>	<i>Cypraea lynx</i>
<i>Lioconcha varians</i>	<i>Cypraea vitellus</i>
<i>Gastrarium scriptum</i>	<i>Cypraea carneola</i>
<i>Gastrarium pectinatum</i>	<i>Ranularia pyrum</i>
<i>Gastrarium tumidum</i>	<i>Monoplex purthenopeum australasiae</i>
<i>Antigona</i> or <i>Periglypta puerpera</i>	<i>Cymatium chlorostoma</i>
<i>Antigona</i> or <i>Periglypta reticulata</i>	<i>Distorsio anus</i>
<i>Chione marica</i>	<i>Bursa granifera</i> (or <i>B. granularis</i>)
<i>Paphia philippinarum</i>	<i>Bursa rubecula</i>
<i>Asaphis deflorata</i>	<i>Ficus ficus</i>
<i>Contumax nodulosom</i>	<i>Murex monodon</i> or <i>Euphylum cornucervi?</i>
<i>Cerithium morum</i>	<i>Murex adustus</i>
<i>Cerithium echinatum</i>	<i>Murex torrefactus</i>
<i>Cerithium aluco</i>	<i>Murex ternispina</i>
<i>Cerithium vertagus</i>	<i>Haustellum haustellum</i>
<i>Cerithium senense obleiscum</i>	<i>Cronia amygdala</i>
<i>Cerithium asper</i>	<i>Phos senticosus</i>
<i>Ovula ovum</i>	<i>Syrinx aruanus</i>
<i>Calpurnus verrucosus</i>	<i>Latirus polygonus</i>
<i>Pustularia cicerula</i>	<i>Latirus nodatus</i> (? = <i>Latirus polygonus</i>)
<i>Pustularia globulus</i>	<i>Peristernia nassatula</i>
<i>Pustularia childreni</i>	<i>Fasciolaria filamentosa</i>
<i>Cypraea staphylaea</i>	<i>Fusinus colus</i>
<i>Cypraea facifer</i>	<i>Fusinus tuberculatus</i>
<i>Cypraea nucleus</i>	<i>Hydatina physis</i>
<i>Cypraea helvola</i>	<i>Conus catus</i>
<i>Cypraea poraria</i>	<i>Conus coronatus</i>
<i>Cypraea erosa</i>	<i>Conus distans</i>
<i>Cypraea annulus</i>	<i>Conus eburneus</i>
<i>Cypraea moneta</i>	<i>Conus ebrenus</i>
<i>Cypraea onyx</i>	<i>Conus figulinus</i>
<i>Cypraea errores</i>	<i>Conus flavidus</i>
<i>Cypraea caurica</i>	<i>Conus generalis</i>
<i>Cypraea punctata</i>	<i>Conus lividus</i>
<i>Cypraea asellus</i>	<i>Conus quericius</i>
<i>Cypraea clandestina</i>	<i>Conus nussatella</i>
<i>Cypraea humphreyii</i>	<i>Conus magus</i>
<i>Cypraea ziezae</i>	<i>Conus marmoreus</i>
<i>Cypraea hirunda</i>	<i>Conus pulicarius</i>
<i>Cypraea chinensis</i>	<i>Conus textilis</i>
<i>Cypraea teres</i>	<i>Conus virgo</i>
<i>Cypraea cribaria</i>	<i>Conus vermiculatus</i>
<i>Cypraea isabella</i>	<i>Chlamys asperrimus</i>
<i>Cypraea testudinaria</i>	<i>Cymbiolacca pulchra</i>

WORMS:

Doris complanata, from between Australia and New Zealand (not
strictly Australian) [planarian].

COELENTERATA:

Medusa pelagica [jellyfish, *Pelagia* sp.]
Medusa radiata [Portuguese man-o-war, *Physalia utriculus*]
Phyllocoeloides velella [= by the wind sailor, *Velella velella*]
beautiful corallines of all colours and figures (Parkinson)
and coral in hull of *Endeavor*
organ pipe coral [*Tubipora musica*]

Banks advocated founding a colony in New South Wales. In time, he said, advantageous return would accrue. In the 1770's, diseases within and escapes from the hulks favoured the plan. In 1786, Lord Sydney initiated preparations with the Treasury. The stage was set for further discoveries of animals in the immediate months and years after the First Fleet arrived in January 1788.

Governor Phillip and his advisers disliked Botany Bay and within a week they had moved to Sydney Cove, leaving the Bay to the two French ships commanded by the explorer La

Table 9.5 Synopsis of the fate of the fauna collected by Banks and others during Cook's first voyage.

GROUP	NUMBER OF SPECIMENS FROM VOYAGE	NUMBER OF DRAWINGS	NUMBER OF EXISTING SPECIMENS	KNOWN PATH OF SPECIMENS LOCATIONS
Mammals	?	40	1?	Skull of kangaroo—John Hunter— Royal College of Surgeons— destroyed World War I Young kangaroo in spirits ?— British Museum
Birds	500	32	12	British Museum—Banks— Royal College of Surgeons Bullock—British Museum British Museum Lever—Vienna Lever—Earl of Derby Lever—Leyden
Reptiles	?	10	1?	Banks—Royal College of Surgeons— British Museum
Fish	500	164	50?	Banks—British Museum John Hunter—British Museum Broussonet—Paris Banks—Bullock—British Museum Banks—Lever—Vienna
Molluscs	?			Often went to private collectors such as Duchess of Portland, Hwass, Alstömer, Humphrey, Cracherode, Fothergill, Hunter, Calonne, Tunstall and others Specimens also in British Museum, Geneva, University of Glasgow
Insects	?		50 drawers full, 500?	Banks—Linnean Society— British Museum Fabricius Hunter
Crustaceans	?	26	40?	Banks—Linnean Society— British Museum
Coelenterates	?			Banks—Royal College of Surgeons Banks—British Museum Fothergill—Hunter— University of Edinburgh

Perouse, who arrived only four days afterwards. Any specimens, drawings or notes of the animals of Botany Bay made by La Perouse and his men were lost when his expedition disappeared at sea on the voyage home.

As Phillip's convicts, military, marine and civil officers and others who made up the complement of the early fleets went about their duty, guarding convicts, building, exploring, farming, making contact with the Aborigines, thieving, drinking, whoring and generally attempting to survive, they came incidentally across animals. At first all were new to them, if not to science, and they were described in journals, letters home and reports (Fig. 9.9). Sometimes the words were illustrated by drawings and paintings. The Europeans perhaps were moved by the same desire for recording that the Aboriginal inhabitants had so many thousands of years before.

Stanbury & Phipps (1980) gathered some of the early words and pictures together. Table 9.6 gives some examples of the way in which the early observers tried to relate to the unfamiliar.

Specimens sent to Europe were pickled in whatever alcohol could be spared or crudely prepared for the six month sea voyage. Governor King's competent aide-de-camp, Ensign Barralier, wrote in his diary for 1802:

"[The Aborigines] brought portions of a monkey (in the native language Colo), but they had cut it in pieces, and the head, which I should have liked to secure, had disappeared. I could only get two feet ... I sent these two feet to the Governor preserved in a bottle of brandy."

Earlier (in 1798), Governor Hunter sent specimens of the wombat and platypus preserved in spirits via Joseph Banks to the Philosophical Society of Newcastle-upon-Tyne. In England and Europe, specialist natural historians examined, dissected, drew, classified, described and named scientifically the specimens, often ill-preserved, which arrived from New South Wales. So far from their native land, strange interpretations often were made and artistic licence abounded. Governor Hunter's wombat, for example, went to the Newcastle Museum. The skin was discovered in a drawer in 1826 and was mounted, sitting on its hind legs like a kangaroo, by the local taxidermist (Fig. 9.10). In this position it was engraved by Thomas Bewick's son to illustrate a publication about the

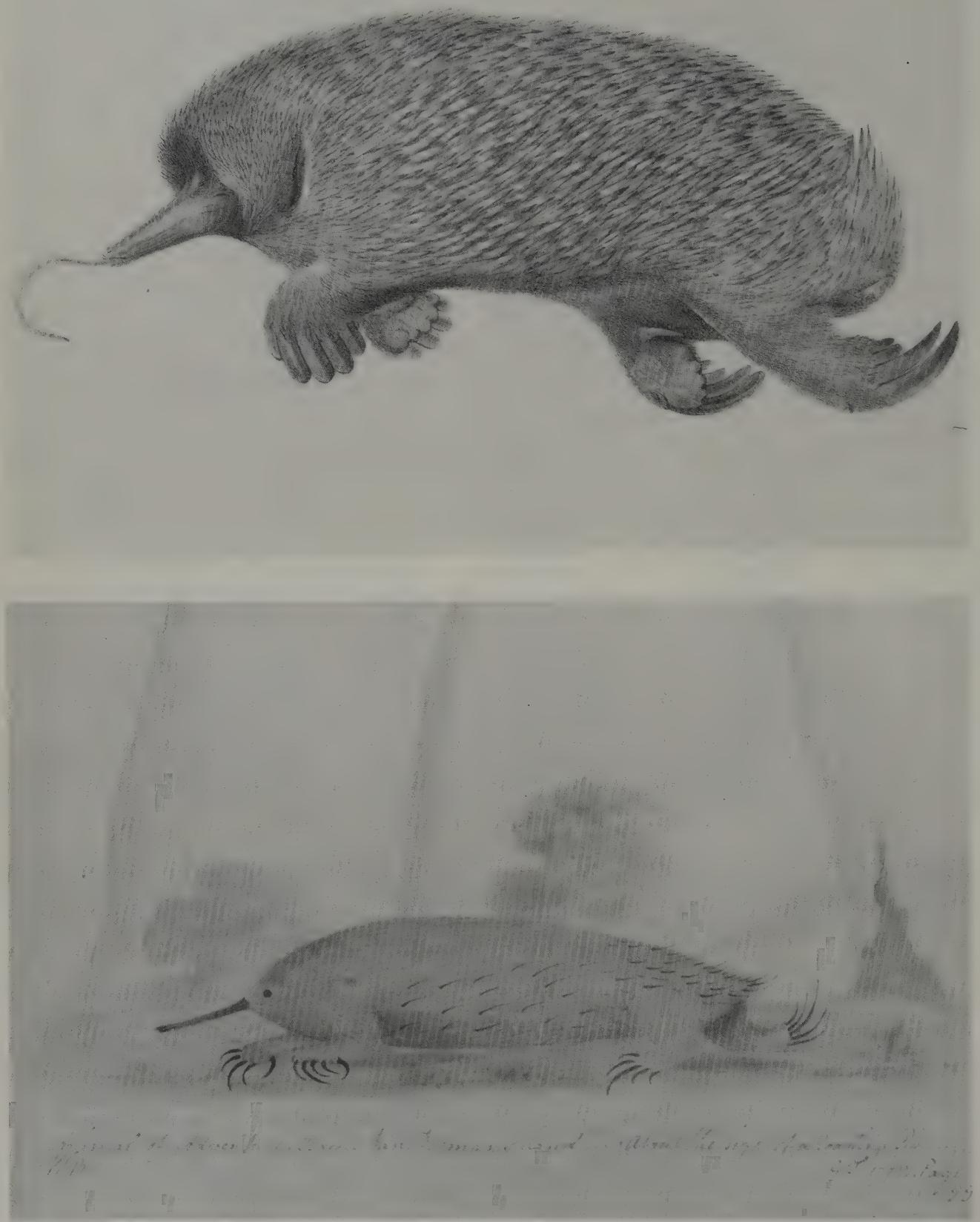


Figure 9.9 Two drawings of the echidna (*Tachyglossus aculeatus*) made on or about 9 February 1792. The more primitive is by George Tobin, Third Lieutenant, under William Bligh's command on the second voyage to obtain breadfruit for the West Indies. The more accomplished is by William Bligh, who sent it to Sir Joseph Banks. Banks arranged for its publication in the Royal Society journal.

Table 9.6 Early descriptions of the fauna discovered by the new settlers soon after their arrival at Port Jackson. Many descriptions relied on the author's knowledge of northern fauna; some were plainly wrong; and some had popular names loosely derived from an Aboriginal word. Even those by professional naturalists such as Shaw of the British Museum were often imprecisely worded or inaccurate.

MAMMALS:

Feb. 1792	George Tobin (lieutenant under William Bligh)	Spiny Anteater	<i>Tachyglossus aculeatus</i>	"a kind of sloth about the size of a roasting pig with a proboscis two or three inches in length"
1793	George Shaw (naturalist at British Museum)	Feathertail Glider	<i>Acrobates pygmaeus</i>	"... not exceeding that of a common domestic mouse"
Nov. 1797	David Collins (Judge Advocate of New South Wales; Lieutenant Governor)	Platypus	<i>Ornithorhynchus anatinus</i>	"an amphibious animal of the mole species ... having instead of the mouth of an animal, the upper and lower mandible of a duck"
Jan. 1798	John Price (servant of Governor Hunter)	Wombat	<i>Vombatus ursinus</i>	"a whom-batt, which is an animal about 20 inches high ... and has much the appearance of a badger"
Jan. 1798	John Price	Koala	<i>Phascolarctos cinereus</i>	"There is another animal which the natives call a cullwine, which much resembles the sloths"
1803	G.P. Harris (deputy surveyor at Port Phillip and van Diemen's Land)	Tasmanian Devil	<i>Sarcophilus harrisii</i>	"These animals were very common on our first settling at Hobart Town"
1805	William Paterson (soldier, naturalist, Governor)	Thylacine	<i>Thylacinus cynocephalus</i>	"... on dissection his stomach was found filled with a quantity of kangaroo"

BIRDS:

Feb. 1788	Henry Ball (sailor)	Woodhen	<i>Tricholimnas sylvestris</i>	"a land-fowl of a dusk brown colour with a bill about four inches long, and feet like those of a chicken"
May 1788	John White (surgeon on First Fleet)	Yellow-faced Honeyeater	<i>Lichenostomus chrysops</i>	"... the size of a martin, and nearly seven inches in length; the bill is broad at the bottom ..."
July 1788	John White	New Holland Honeyeater	<i>Phylidonyris novaehollandiae</i>	"We discovered the New Holland Creeper ... the size of a nightingal"
1792	George Shaw	Eastern Rosella	<i>Platycercus eximus</i>	"long tailed variegated parrot with head, throat, breast and vent crimson"
1797	John Wilson (convict who lived with Aborigines)	Superb Lyrebird	<i>Menura novaehollandiae</i>	"a bird of the pheasant species"

REPTILES:

1790	George Shaw	Red-bellied Black Snake	<i>Pseudechis porphyriacus</i>	"this beautiful snake ... not of a poisonous nature ... on the upper parts is a glossy violet-black; the sides of an elegant deep crimson"
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FISH:

Nov. 1789	Arthur Phillip	Wobbegong Shark	<i>Orectolobus maculatus</i>	"Having lain on the deck for two hours seemingly quiet, on Mr Watt's dog passing by, the shark sprung upon it with all the ferocity imaginable"
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contents of the museum. In 1884, the wombat was transferred to the Hancock Museum where it remains today, still begging patiently (Turner, 1980).

Most of the First Fleet journals and related publications contained some reference to the fauna. John White's *Journal*

of a Voyage to New South Wales proved important, as the zoological notes were edited by George Shaw and John Hunter. Shaw was later to bring out the *Zoology of New Holland* (1793) and Hunter's observations may have been used after his death by Home (1795) in speculations about the manner of reproduction of kangaroos.



Figure 9.10 Governor Hunter sent a wombat to Joseph Banks in 1798. From there it went to the Philosophical Society of Newcastle-upon-Tyne, where the skin was examined by the erudite. In 1826 it was found in a drawer in the Newcastle Museum and was mounted by mistake sitting up like a kangaroo. [courtesy Hancock Museum]

Table 9.7 Some French expeditions to Australia on which animals were sighted, collected or drawn.

EXPLORER	DATE IN AUSTRALIA	PLACE VISITED
Marion du Fresne	1772	Tasmania
François St Allouarass	1772	Western Australia
Jean La Perouse	1788	Botany Bay
Joseph d'Entrecasteaux	1792, 1793	Tasmania, Western Australia
Nicolas Baudin	1801, 1802, 1803	Western Australia, South Australia, Tasmania, Sydney
Louis de Freycinet	1818, 1819	Western Australia, Sydney
Louis Duperrey	1824	Sydney
Jules d'Urville	1826, 1827, 1828	Western Australia, South Australia, Sydney, Tasmania

SECOND WIND - THE BEGINNINGS OF AUSTRALIAN ZOOLOGICAL SCIENCE

When the thrill of the discovery of Australia by Europeans and the novelty of seeing strange animals had lessened, the work of describing the fauna was carried out with more attention to detail. Secondary voyages of discovery, especially those sent from France (see Table 9.7), inland expeditions and collectors especially paid and trained, gradually built up a respectable body of knowledge.

Captain Bruni d'Entrecasteaux and his ships *Recherche* and *Esperance* visited Australia in 1792 and 1793. He had been instructed to search for La Perouse who had disappeared at sea after leaving Botany Bay in 1788. On board d'Entrecasteaux's ships were two naturalists: Jacques Labillardiere, who described the Cape Barren Goose, *Cereopsis novaehollandiae*, the Ground Parrot, *Pezoporus wallicus* and other birds, mammals and fishes; and Claude Riche, who collected many insects. The expedition failed to find any trace of La Perouse. D'Entrecasteaux and others died at sea or were imprisoned on the return voyage. Nevertheless, the specimens collected did eventually safely reach the museums of Paris.

One of the most successful collecting voyages was that commanded by Nicolas Baudin in the *Géographe* and Jacques Hamlin in the *Naturaliste*. Both men were interested in natural history, collecting, observing and generally taking an interest in the work of their collector, François Péron, and that of their artist, Charles Lesueur. They visited Australia in 1801–1803 and amassed 18,414 specimens. Working on their haul, zoologists in the Natural History Museum in Paris identified 3,872 different species, of which 2,545 were new to science. Lesueur made nearly a thousand paintings and drawings from life (Fig. 9.11).

Some of Péron's assistants died on the voyage; Stanislaus Levillain died in 1801, René Mauge in 1802 and Baudin on the voyage home in 1803. The loss of people to whom the scientists could turn for first hand information when unpacking the specimens and interpreting notes must have made the job of identification difficult. Péron was in charge of the official record of the voyage, but he too died in 1810 before the second of three volumes could be completed. In consequence, the work of the expedition has not received the attention that it might. Papers on the expedition are few relative to its scientific importance; in spite of some being in languages other than English, the subject appears to be one into which research is warranted. Lesueur's paintings of animals still rival any made and that they have not been studied and reproduced more often is surprising.

Diligence is required to track down many of the animals collected and named scientifically (if not first discovered) by Péron and other early naturalists. A small wallaby was named *Thylagale eugenii* in 1817 by Desmarest after it had been collected by Péron from an island off the South Australian coast. The same species, however, had probably been seen by Pelsaert in 1629 and, because of the range of colour variations, it received various other scientific names after 1817, including *Thylagale flindersi*. It is now *Macropus eugenii*.

The Emu, *Dromaius novaehollandiae*, was first seen by Europeans of the First Fleet. Then known as the New Holland Cassowary, one was shot and brought into the settlement in February 1788, but its scientific naming had to wait until 1790 when Latham called it *Casuarius novaehollandiae* after an illustration had appeared in Arthur Phillip's *Voyage to Botany Bay* in 1789.

King and Kangaroo Islands at this time had species of dwarf emu. They were seen by both Flinders and Péron. In 1803, six pairs were brought to Sydney by William Moody from



Figure 9.11 Charles Lesueur's illustrations published in the account of Baudin's voyage (1807) were the finest of their time. Only a few appeared in print, although he made thousands on the voyage.

King Island, but four pairs died on the way. In 1907 this species was belatedly named *Peronista peroni* (now *Dromaius minor*). It became extinct on King Island in 1805 and on Kangaroo Island in 1827 due to the activities of sealers and whalers.

Péron and Lesueur were also responsible for the first scientific description of the Australian Sea Lion (*Neophoca cinerea*) (which they saw on Kangaroo island in 1802) and the Elephant Seal (*Mirounga leonina*) which was then plentiful on the shores of Tasmania.

The courageous marine explorers, George Bass and Matthew Flinders, also noted the seals when they discovered Bass Strait in 1797–98 and correctly predicted industries might arise around both the seals and mutton birds (*Puffinus tenuirostris*).

The difficulties awaiting the first zoologist to tackle systematically an account of the discovery and naming of all Australian fauna are compounded after the turn of the 18th Century by the addition of extensive land explorations to those undertaken by sea. Table 9.8 places some of the former in relation to the establishment of museums in Australia and other relevant events.

As several accounts of the discoveries of animals in the early 19th Century have been published, either dealing with specific groups, such as insects (Musgrave, 1930) or birds (Whittell, 1954), or in general (Fletcher, 1901; Finney, 1984), there is no point in repeating them here. The accounts show clearly how little coordination there was between the various expeditions. Even when collections were made the specimens often were handled carelessly unless they were acquired by a

dedicated private collector such as Alexander Macleay. Macleay thoroughly understood the necessity for the long term future of natural history collections and made adequate provision in his will for the years of labour expended on his collection (Fig. 9.12).

Macleay was influential in the formation of the first public museum in Australia, the Australian Museum in Sydney. The pattern of the foundation of museums in Australia and the activities of their staff well illustrate the three phases of activity suggested by Bassalla (1967) in the evolution of the science of a newly discovered country. They are (i) a source for European science, (ii) colonial science and (iii) a struggle to achieve an independent scientific tradition.

Bassalla's trends can be traced by consideration of three members of the Macleay family: Alexander, his son William Sharp and his nephew (later) Sir William.

Alexander Macleay joined with Thomas Marsham and Dru Drury in advancing Lewin money to travel to and collect in New South Wales. The return was expected to be in specimens and data. So, in 1804–5 Macleay was composing the descriptions for Lewin's *Prodromus Entomology - Natural History of Lepidopterous Insects of New South Wales*, while Lewin's contribution was to draw and engrave the illustrations (Fletcher, 1921).

Alexander's son, William Sharp, also described insects from Australia in his *Horae Entomologicae* published from 1819–1821 and in 1826 catalogued the insects collected by P.P. King on his various voyages around the northwest of Australia.

9. DISCOVERY AND COLLECTIONS

Table 9.8 Inland explorations of Australia and contemporary events concerning the collecting of fauna and the foundations of museums in Australia.

DATE	EXPLORER	DESTINATION		CONTEMPORARY EVENTS
1800–1820	Barrallier, Caley, Blaxland, Lawson, Wentworth, Evans, Oxley, Howe, Harris, Brown, Collins, Beaumont	Picton, Bathurst, Mt Banks, Newcastle, Pt Macquarie, Tasmania	1805 1808	Donovan's <i>Insects of New Holland</i> published; Lewin's <i>Lepidopterous Insects of New South Wales</i> published Lewin's <i>Birds of New South Wales</i> published
1821–1830	Curries, Hume, Hovell, Cunningham, Sturt, Hellyer, Oxley	Canberra, Melbourne, Darlings Downs, mouth of the Murray River, Tasmania	1821 1826 1829	Philosophical Society inaugurated in Sydney Alexander Macleay arrives in Australia; William Sharp Macleay publishes entomological catalogue of King's voyage First curator of the Australian Museum appointed
1831–1840	Mitchell, Sturt, Strzelecki, Eyre, Grey	western New South Wales, Victoria, Mt Kosciusko, South Australia, coastal Western Australia	1837 1840 1841	Adelaide and Melbourne named Gould's <i>Birds of Australia</i> published Lady Franklin's private museum opens in Hobart
1841–1850	Sturt, Leichhardt, Mitchell, Kennedy, Roe, Gregory	South Australia, Queensland, Northern Territory, coastal Western Australia	1842 1845 1847	Brisbane (Moreton Bay) opened to settlers Gould's <i>Mammals of Australia</i> published <i>Diprotodon</i> skeleton shown in Sydney
1851–1862	Gregory, Babbage, Burke and Wills, Stuart	Queensland, Northern Territory, South North crossing, coastal Western Australia	1854 1859 1860 1862	First curator of National Museum, Melbourne Queensland separated from New South Wales First curator of South Australian Museum Rooms provided for the Queensland Museum; Entomological Society of New South Wales founded
1863–1875	Forrest, Giles, Warburton, Gosse	Central Australia and inner Western Australia	1863 1869 1874 1875	Royal Society of Tasmania's Museum opens Kreft publishes <i>Snakes of Australia</i> Linnean Society of New South Wales founded William Macleay's expedition to New Guinea

At the beginning of the same year, Alexander came to Sydney as Colonial Secretary. He brought most of his son's collection of insects with him as well as his own. Kept busy by his official duties and establishing plants on a grant of land at Elizabeth Bay where he was to build a house, he still managed to send the Linnean Society of London, which he had served as Secretary for twenty-five years, a consignment of colonial birds.

Alexander Macleay's activities in Australia mark the beginnings of Bassalla's phase two, colonial science. In 1822, the Philosophical Society of Australasia failed, only a year after its establishment, in spite of Governor Brisbane's presidency. The timing of the formation of the society – 1821 – may have been a little early, for there were at that time few *bona fide* scientists in the colony. Members of the society included men of medicine, business, the sea and the church, but not one scientist, in spite of the already functioning Botanical Gardens, established in 1816 and the Parramatta Observatory (1822).

With Macleay's arrival, the scene changed. Lord Bathurst wrote to Governor Darling in 1827 authorizing the expenditure of up to £200 per annum towards the establishment of a public museum. Macleay may have been one of the persons who influenced Bathurst to approve the appointment of a zoologist (on the same pay as the Colonial Botanist). The collections of the Philosophical Society had been housed in a room in the Colonial Secretary's Office, where Macleay undoubtedly would have inspected them in 1826.

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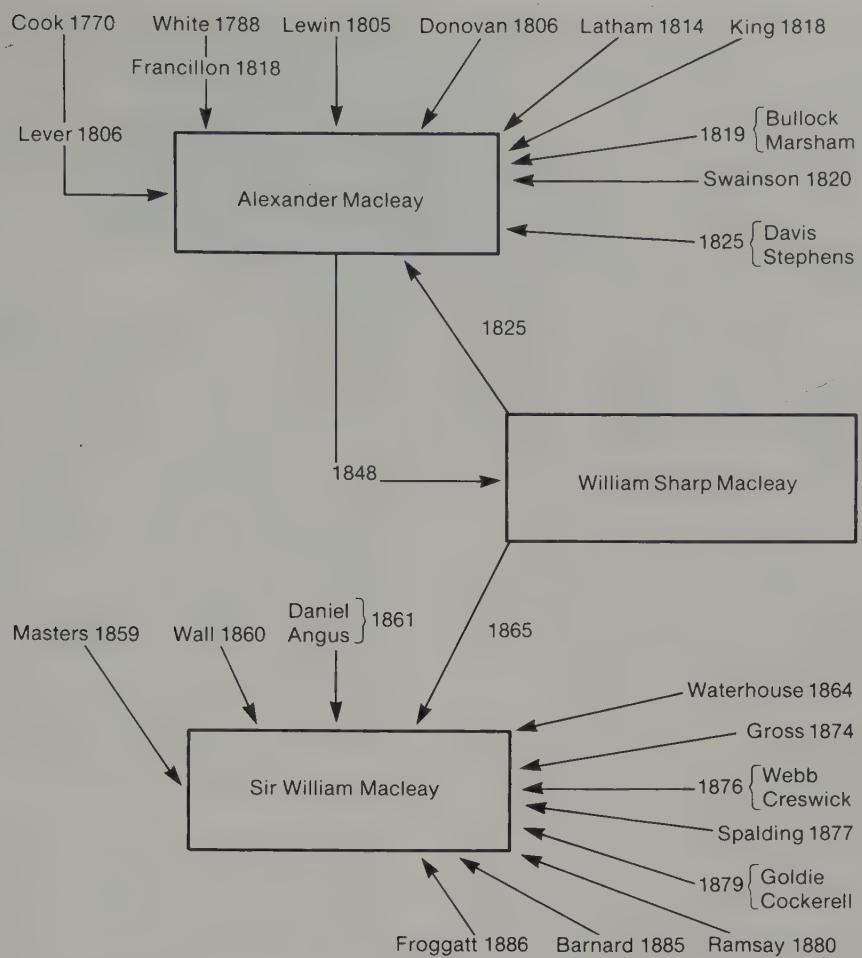


Figure 9.12 Diagram showing the origin of some of the specimens in the Macleay family collections.

The first staff member of the Australian Museum, William Holmes, at one time a carpenter and joiner, was appointed on 16 June 1829 by Darling or perhaps by Macleay (Strahan, 1979). Holmes' qualifications suited him for the job of moving specimens from the Colonial Secretary's Office to a shed attached to the Judge Advocate's old office and installing them in appropriate cabinets. Soon, Holmes was at least officially called a zoologist. The era of colonial zoology had begun officially. On 24 August, 1831, he accidentally shot himself at Moreton Bay collecting "birds and other curiosities".

The third member of the Macleay family to be involved in the Australian zoological scene was William Macleay, William Sharp's cousin. Sir William inherited the family insect collection, but also greatly expanded the collection in all areas of fauna, geology and anthropology. In 1875, he bought a ship, the *Chevert*, and mounted a collecting expedition to New Guinea.

The event caught the public imagination and although the unrealistic hopes entertained for the work of the expedition brought about public disappointment and disenchantment on Macleay's return, he believed that, considering the difficulties, he had done well. Macleay was vindicated when he gave the collection to Sydney University in 1888, by which time it had achieved a reputation as the best natural history collection outside of the British Museum. His work in founding the Entomological Society of New South Wales in 1862 and the Linnean Society of New South Wales in 1874 further

marked his desire to achieve an independent scientific tradition for the natural sciences (Bassalla's third phase of development).

THE ESTABLISHMENT OF STATE MUSEUMS

Nearly all public collections and museums in Australia had shaky early years. Four main museums were established by the 1860's: in Sydney, Melbourne, Adelaide and Brisbane. Essentially, they were started by enthusiasts, often banded together under the guise of a Philosophical Society. Once the government had been persuaded to provide space and salary, the die was cast. Collections were moved from place to place as exhibits accumulated. In depression years, building plans were shelved, staff retrenched, salaries cut and the collections suffered. As most specimens were on display, collection and other data were frequently lost, colours faded and deterioration set in as poor preservation and *Anthrenus* beetles took their toll.

Even after curators began to retain the most important specimens in the colony, many more specimens were lost. A few were stolen, for the trade in specimens such as the Night Parrot (*Geopsittacus occidentalis*) was lucrative. Duplicates of marsupials and native birds were exchanged for common overseas species in the mistaken assumption that the stocks of Australian animals were inexhaustible.

9. DISCOVERY AND COLLECTIONS

The first purpose-built buildings in Australia soon proved inadequate. They were built when money was in good supply, which meant that the building proceeded hand in hand with the purchase or collection of large numbers of specimens and/or the hiring of staff. Consequently, the buildings proved too small as soon as staff moved the collections in and started to prepare exhibits. Nevertheless, men such as Gerard Krefft in New South Wales, Frederick McCoy in Victoria and Charles De Vis in Queensland managed to lay the foundations of the public collection in Australia through their resolve to achieve their vision whatever the personal cost.

Private collectors such as the Ramsay (mainly birds) and Macleay families (insects and later all species) were less subject to financial reverses and their collections grew steadily, sometimes as the result of exchanges and other transactions with public museums.

The Australian Museum

The beginnings of The Australian Museum show common human failings. Underneath the basic drive to collect, display and build can be discerned greed, social ambition, inexperience and tolerance of an unsatisfactory state of affairs.

Sydney's first curator, the ex-carpenter William Holmes, seems to have used his skills to fit up the shed which served as the Museum. It was called "a beautiful collection of Australian curiosities" and was "politely" shown "to any respectable individuals who may think fit to call" "between the hours of ten and three" (*Sydney Gazette*, 1830).

The curatorship then fell to an ex-convict, William Galvin, mainly because he was a messenger in the office of the Clerk to the Legislative Council and happened to be handy. A convict, John Roach, who accompanied Mitchell on collecting trips was taxidermist and was referred to by his companions as that "rascally bird-stuffer."

Roach remained on the staff until 1840, but Galvin was replaced by a well travelled physician and amateur naturalist, Dr. George Bennett, who became secretary and curator. He had visited Sydney in 1829 and 1832 and arrived to settle in 1835. Bennett hoped to make a living out of his hobby, natural history, but the salary was insufficient and in 1841 he resigned to take up the more lucrative employment of medicine.

During Bennett's reign, the Museum was moved to a third home (it had been moved under Galvin) and a catalogue of specimens was compiled. The Museum then had: 36 mammals, 317 birds, five reptiles, six fishes, 211 insects, 25 molluscs and nine Aboriginal artefacts.

Just after Bennett joined the Museum, its name was changed from Colonial to Australian and trustees, or rather a committee of superintendence, was appointed. Among these were Alexander and George Macleay, Deas Thompson (Clerk to the Legislative Council who later replaced Alexander Macleay as Colonial Secretary), P.P. King and Charles Sturt.

The geologist Rev. W.B. Clarke was appointed a trustee in 1840. In 1841, he and a practical naturalist, William Wall, succeeded Bennett. One of Clarke's first jobs was to superintend yet another move of the collection, this time to Woolloomooloo. He attempted to carry on his duties from Parramatta. His paid position was abolished in 1843, although he remained a trustee until 1874.

Wall's skills may perhaps be ranked in order as naturalist, survivor, organizer. In 1844, he spent five months on an inadequately funded collecting expedition to the Murrumbidgee, then a squatting area. Within days the expedition was short of transport, food and money. He nearly starved, hav-

ing to seek charitable handouts and leave IOU's. He collected 136 birds and sixteen mammals before the government sent money for his return journey.

In 1847, Wall, Bennett and Leichhardt assembled the *Diprotodon* which was exhibited for a short time until it was sent to England. The success of his temporary exhibition encouraged Wall to mount a skeleton of a whale which was displayed outside the Museum in 1849 where it attracted considerable attention.

Wall's privations on his 1844 expedition may have demonstrated the devotions of naturalists to the cause, for in 1845 money was voted by the Legislative Council to erect a purpose-built museum building. Welcome though this move might have appeared at the time, it proved to be at least as great a disaster as the expedition. The building was started in 1846, but the amount of money set aside was inadequate. In 1849, the Colonial Architect resigned under criticism, but funds were only grudgingly released. The outside was not finished until 1852 and the inside until 1857.

During the building, the powers of the trustees had been increased, as had their numbers to twenty-four. By 1853, a position of Secretary was established and filled by George Angus at a salary of £50 greater than Wall's who for eight years had been the senior employee. Wall's private accommodation within the Museum was reduced severely and after a row over keys in 1858, Wall resigned, bringing to a head the fact that the newly finished Museum was totally inadequate for the collection.

Happily (but not entirely properly), Governor Dennison became a trustee. He was prepared to smooth the way for the progress of the Museum. Soon, money was available to seek a well-qualified curator overseas and Angus gave notice.

Simon Pittard, a protégé of Owens, was appointed Curator and Secretary and Gerard Krefft Assistant Curator and Clerk in 1860. In 1861, Sir William Macleay replaced Dennison as trustee and Krefft replaced the now deceased Pittard.

Krefft, formerly a collector for the National Museum in Melbourne, was practical, an able administrator and a hard working naturalist. His appointment marked a turning point for the Australian Museum's scientific reputation. Krefft published, with some aid from his own pocket, *The Snakes of Australia* (1869), *Mammals of Australia* (1871), *Australian Fossil Remains in the Australian Museum* (1870) and *Minerals and Rocks in the Australian Museum* (1873). He found and kept a second *Diprotodon* skeleton (a first having been sent overseas). Also, he published the first description of the lungfish, which he did with an eye for publicity, in a letter to the *Sydney Morning Herald* (17/1/1870).

At this time, the Australian Museum gained a reputation as an international scientific institution and started a period of great growth for the collections. No longer could all specimens be placed on public display.

One of the most assiduous collectors for the Museum was George Masters who joined the staff in 1864 (Fig. 9.13). His trips included:

- 1864 Interior of New South Wales;
- 1865 Queensland; Flinders Ranges, South Australia;
- 1866 King George Sound;
- 1867 Tasmania; Wide Bay, Queensland;
- 1868-9 Western Australia;
- 1869 Lord Howe Island;
- 1870 Maryborough, Queensland.

As expected, Krefft's professionalism drew him into conflict with the trustees, some of whom regarded the Museum as a club and its specimens as a resource for their own collections, a just reward for their influence and time spent in



Figure 9.13 A collecting reference for George Masters during his 1868–1869 trip to Western Australia, signed by Deas Thomson, Krefft and Masters.

meetings. In 1874, he was called upon to resign after a theft by a member or members of the public, the finding of indecent photographs in the workshops, occasional intoxication and other matters. He refused, claiming that although trustees had power to recommend his appointment they had no power to sack him. After some months of legal battle he was carried out of his private apartment in the Museum on a chair by two bailiffs hired by trustees. Two of the scientific trustees, Bennett and Clarke, resigned over the matter, clearly supporting Krefft. Krefft won a civil suit, but was not reinstated and died in 1881 in debt, an embittered man.

Alexander Macleay had been influential in the early days of the Australian Museum. Now, it was William Macleay's turn. Significantly, he did not resign as trustee after Krefft was removed. With hindsight, it seems obvious that not only was he behind the dismissal, but also attracted George Masters to the position of Curator of his own private collections and pushed Edward Pierson Ramsay into the position vacated by Krefft.

Ramsay effectively led the Museum for nearly twenty years. His interest in ornithology is reflected in the fact that the Museum acquired over 18,000 bird skins during his tenure. He was a successful collector of other items, as well; within five years he replaced the 2,000 ethnographic artefacts lost in the Garden Palace fire of 1882 with 7,500 new specimens. In 1883, he went overseas and bought a large collection of fishes from Francis Day, who had a disagreement with the British Museum.

Most importantly perhaps, Ramsay managed to increase the scientific staff of the Museum by a series of subterfuges involving the employment of cataloguers and then upgrading them to assistant in a specific discipline. By 1878, these included John Brazier (molluscs), Thomas Whitelegge (marine invertebrates), A. Sidney Olliff (insects), John Douglas Ogilby (vertebrates), Alfred J. North (birds) and Robert Etheridge (palaeontology). The scientific staff were supported by nineteen other employees.

Interestingly, Brazier joined the Queensland Museum in 1889, but not liking the facilities there, moved to Sydney. Ogilby, although an excellent zoologist, was rather fond of alcohol. He was dismissed in 1890 and in 1907 joined the Queensland Museum where the specimens were preserved in formalin.

One of Ramsay's important initiatives was the *Records of the Australian Museum*, which commenced in 1890. Ramsay's contributions came to an end in 1893 when he became sick. A financial embarrassment caused the government to cut the funds for the Museum from £11,000 in 1892 to £4,000 in 1893. Not only were staff reductions inevitable, but salaries were also cut and neither the new Curator, Etheridge (appointed 1895) nor the Trustees seemed able to protest sufficiently vigorously. Long after the government's emergency had passed, salaries remained low until forced up by the labour shortages during World War I.

9. DISCOVERY AND COLLECTIONS

Table 9.9 Early purchases for the National Museum of Victoria. (Figures taken from Prescott, 1954)

YEAR	SPECIMENS REQUESTED OR ACQUIRED	FROM	SUM PAID
1857	Invertebrates	J.O. Westwood London	£250
1857	Birds	J. Gould, Royal Zoological Society	£400
1857	Mammals, reptiles, fish, echinoderms, shells, corals	J.E. Gray, British Museum	£520
1857	Skulls and skeletons	R. Owen, Royal College of Surgeons	£30
1857	Shells	C. Thatcher, Bendigo	exchange for duplicates
1857	143 birds	Boston Society of Natural History	?
1859	Insects of Victoria	?	£100
1862	Egg of <i>Aepyornis</i>	Laffarque, origin unknown	£100
1862	Molluscs	Lovell Reeve	£500+
1862	3 000 Hymenoptera and many other insects	F. Walker, London	1/- per specimen
1862	A series of gorillas	E. Gerrard, London	?
1863	38 665 insects	John Curtis, London	£567
1865	Molluscs, cirripedes, Crustacea, arachnids and myriapods	Lith de Jeude	£4 004

Perhaps to find cheap labour, a system of cadetships was introduced into the Australian Museum in 1908. The salary offered was less than one tenth of that of a biologist with a degree. While some cadets appointed became extremely knowledgeable in their chosen field, their breadth of understanding of some of the newer developments in biology was limited and the concepts offered to the public by the Australian Museum, and other museums in Australia for that matter, were principally taxonomic until after World War II.

The National Museum, Victoria

Krefft is a link between the Australian Museum and the National Museum in Melbourne, for he served both. The National Museum of Victoria (now the Museum of Victoria) demonstrates the determination and staying power of one man, its honorary director, Frederick McCoy (Prescott, 1954).

McCoy was the second appointment. The first was William Blandowski, an ex-corporal from Prussia about whom little is known but that he had previously made a trip to Cape York to collect natural history specimens. Appointed in April 1854, he was in the field in June and November and only eight months after his appointment had 230 different specimens of birds in the collection. He also had written reports on geological and ethnological matters. Blandowski was instrumental in forming the Philosophical Society of Victoria, the members of which contributed specimens to the Museum.

The collection was at that time housed in two rooms in the Surveyor-General's office. In 1855–56 there was a crisis in government funding and the two rooms were required. In May 1856, McCoy, Professor of Natural Science at Melbourne University since 1854, was appointed Palaeontologist to the Geological Survey of Victoria. McCoy saw the opportunity to have specimens adjacent to his students and took the collection to the University while Blandowski was

on an eight month long field trip. Blandowski was a man who took offence easily. Even before he left on the trip, there had been acrimony between the two. Of fifteen men engaged to accompany him only one, Krefft, did not leave the expedition because of the way it was run. So far as collecting goes, Krefft and Blandowski (or the Aborigines they met who were paid one shilling a skin) did a good job, bringing back 16,000 specimens, although many of them must have been duplicates and invertebrates.

On his return, Blandowski refused to go to the University or his office and had the specimens and drawings from the trip sent to his private rooms.

Then followed a scandal. It started because he named some new species of fish after council members of the Philosophical Society. Unfortunately, his descriptions of the fish ("low forehead, big belly and sharp spine" and "slimy, slippery fish, lives in the mud") were taken to refer also to the councillors. Blandowski refused to amend the offending passages; council retorted by refusing to publish the relevant pages.

When Blandowski later refused to deliver the specimens and drawings made on the trips, which had cost the government £2,000, his reputation was in tatters. He left with most of the specimens for Germany in 1859 and some of the material was published there.

When McCoy brought the nucleus of the National Museum to the University, the specimens were installed in four specially built rooms. There was a public outburst against the move, but it was a *fait accompli*. McCoy set about making it the best collection in Australia by purchasing large consignments of specimens from overseas (Table 9.9). Almost until his death in 1899, McCoy was the sole scientist on the staff. There were others in the capacity of secretary, taxidermist, keeper and assistant, but McCoy managed the Museum, undertook his professorial duties (later his chair was divided into three) and advised the government on many matters.

McCoy continually requested funds from the government for staff and specimens. After the University approved a 160 feet square space for a building, he requested money for a museum, too. For some years, he was remarkably successful in having funds approved and by 1863 he succeeded in making the final payment on a well-planned museum building. Not all the collection would fit into it, however, and as McCoy was being requested by the University to vacate the two rooms owned by them in which the remainder of his specimens were stored, he approached the government again for funds. McCoy was given ultimatum after ultimatum to vacate the space and he sent letters to the government year after year until 1869. The University struck the final blow by planning an examination in the storage rooms. McCoy had to submit, although by this time the annual visitor numbers had risen from 30,218 in 1859 to 84,689 and he complained that the collections were so crowded as to receive "daily injury".

In 1870, eighteen trustees were appointed for all Victoria's museums, the library and gallery. McCoy had to give to the newly formed Industrial and Technological Museum his mining and agricultural exhibits which he had been collecting as assiduously as the zoological and geological ones. Furthermore, McCoy's title was changed from director to curator and his funding was reduced so severely that he was obliged to cancel many of his overseas orders.

From 1874 to 1878, McCoy published his *Prodromus of Palaeontology and Zoology*, a work which he had planned in the late 1850's and which kept him busy during the financially difficult years. By 1877, however, he was asking again for money to complete the Museum and he once again started to buy from overseas and to acquire Australian specimens. In spite of his persistence, the Museum was never completed, although in 1898 the sum of £7,500 was allocated. In 1899, McCoy died and the natural history exhibits were moved to the public library building in Swanston Street.

The South Australian Museum

Only two years after the State's foundation in 1837, specimens were collected towards a future museum, including "native" weapons, shells and a copy of Gould's synopsis (*South Australian Gazette*, 1839). The Adelaide Philosophical Society (founded 1853) pushed strongly for an institute containing a museum.

A board of trustees was set up in 1856 to control a library and museum to be called The South Australian Institute. Once the Act passed, further collections were offered and the trustees could say in 1857, "extensive collections of great and varied interest await only a room for their reception".

An institute building, a part of which belonged to the Museum, opened on 29 January 1861. The first curator, Frederick Waterhouse, aged 45, had been appointed in the previous year. He was the youngest brother of the first curator of the Entomological Society of London. He had collected numerous specimens since his arrival in Australia in 1852. Waterhouse set up the first exhibitions in a single room in 1862.

One of the Museum's first purchases were sets of Gould's Mammals and Birds. One of the first collecting trips was to Kangaroo Island. Another early one was far more adventurous, as the naturalist accompanying Sturt's expedition, Waterhouse found the first specimens known to science of the Princess Alexandra Parrot (*Polytelis alexandrae*).

The collections started to grow after 1863, as Table 9.10 shows, and Waterhouse willingly (though with hindsight some might say wantonly) exchanged many South Australian specimens for overseas or interstate material. Hale (1956) estimates that at least 2,000 bird skins were exchanged, but

Table 9.10 Numbers of specimens in the South Australian Museum in 1863 and 1867. (Figures from Hale, 1956)

GROUP	NUMBER OF SPECIMENS	
	in 1863	in 1867
mammals	20	170
birds	200	500
reptiles	25	?
fish	20	?
insects	2 000	?
molluscs	2 000	?

at least some of the material retained was or is now valuable (Moa skeleton, Thylacine). Other material left South Australia for international exhibitions at the request of the government. In most years, funding was relatively poor. For example, in 1866, £500 had to include salaries and expenditure, so Waterhouse's exchange programs can be understood as a means of providing the Museum with a representative collection.

The exhibitions and storage conditions seem to have been poor. In 1876, Waterhouse was supplied with an airtight box and chloroform to deal with attacks of *Anthrenus*. The public complained that too many specimens were crowded in the exhibition cases.

With the enlargement of the collections from about 1863, more room was necessary. At first, the corridors leading to the Museum were utilized; in 1867 an additional room was acquired when the School of Design moved out of the Institute building. Soon, further space was imperative. In 1872, the Parliament passed a vote of £3,000 towards a shared ancillary building in which the Museum was to occupy the top floor. Footings were laid in 1873. Then, the government initiated an inquiry at which Waterhouse explained that he wanted a separate building and that to display properly the specimens 800 linear feet of wall cases were needed.

Parliament voted sums of £5,000 and architects were asked to prepare plans in 1874 and 1876. In 1879, work started on a west wing of the Institute. In 1882, the collections were moved. Waterhouse retired and George Beazley was appointed Assistant Curator and Taxidermist and Wilhelm Haacke, Curator.

Haacke had worked in museums in New Zealand and set about making a fresh start for the South Australian Museum. In 1883, he persuaded the trustees to allow him to use the title Director. He threw out all the tired old specimens, telling the trustees that provision must be made for new ones. A collector, F.W. Andrews who previously had sold items to the Museum, was appointed permanently. An entomological collector, Gottlieb Teffer, was engaged. Amandas Zietz became preparator, Otta Rau a taxidermist and Otho Noake labourer and attendant.

Haacke organized local amateur collectors and had printed 500 copies of a collector's manual, *A Scheme for the Organization and Direction of the Efforts of Amateur Collectors*. He drew up a plan of exhibits for the new wing which was to be opened in 1884. His position, however, was undermined by dissension among the staff, controversy over his destruction of specimens and much public criticism of his extensive exchange programs (in one he sent away over 1,000 specimens on the basis of promises). After his resignation on

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1 November 1884, only twelve Australian mammals and 60 birds were found suitable for exhibition. The new wing was opened on 18 December 1884.

Just prior to Haacke's departure, the board of Trustees of the old Institute was revamped and given responsibility for the Public Library, Museum and Art Gallery. The Chairman of the Museum sub-committee, Dr Edward C. Stirling, presided over the Museum as Chairman, Honorary Director or Director until 1914. During this time the Museum grew in status. Before the turn of the century important collections and discoveries were made including the discovery of the Marsupial Mole, *Notoryctes typhlops* and the collection of skeletal material of *Diprotodon* and the giant wombat, *Phascolonus gigas*. Several important expeditions were undertaken, such as the Elder Exploring Expedition of 1891-2 and the Horn Expedition of 1894. Dioramas were erected in the Museum and at overseas exhibitions. In 1892-3, a new wing was erected devoted wholly to the Museum.

The Queensland Museum

The South Australian Museum acquired significant regional collections from Kangaroo Island to the centre of Australia. Queensland, relatively near Cape York and New Guinea, was also in a good position to specialize.

Queensland was separated from New South Wales in 1859 and in the same year the Queensland Philosophical Society was formed, that frequent precursor to state museums in Australia.

In 1862, the government lent rooms in a disused windmill on Wickham Terrace (now the oldest surviving building in Brisbane). The Society advertised for "specimens of natural history for classification and arrangement". At first, the Museum was run by the members. Its premises were poor. In 1868, after some specimens were damaged by rain, the collection was moved to the old Parliamentary building.

The Vice-President of the Society, Charles Coxen, seems to have been the driving force behind the development of the Museum (Mather, 1986). Coxen came to Australia in 1833 to collect bird specimens. His brother-in-law was John Gould, which helps explain the early emphasis on ornithological collections in the Museum.

In 1870, the displays consisted of at least 200 birds, shells, two cabinets of insects, a case of fossils, as well as minerals. Coxen was formally appointed Honorary Curator in 1871.

The collections were moved to larger premises in 1873 in the Old Post Office and an assistant, Karl Staiger, was paid from government funds. Just before Coxen died in 1876, a board of trustees was appointed and Staiger remained in charge until 1880. He supplemented the displays with living animals, including snakes and lungfish (in the nearby Botanical Gardens).

Coxen's widow, Elizabeth, offered her services to the Museum, which were accepted on a part-time basis. She collected, arranged exchanges and worked on the molluscs. Mrs Coxen seems to have been the first woman employee of any museum in Australia and perhaps the first to regularly attend the meetings of scientific societies.

The trustees were successful in acquiring extra rooms in the Old Post Office as other tenants moved out and the collections grew. In common with other Australian museums, specimens and collections from overseas were bought or exchanged. The aim was to try to obtain one of everything rather than intentionally specialize in one or two groups or a district.

In 1878-79, a purpose-built museum was completed. William Haswell was appointed curator in June 1880. The trustees unwisely tried to save money on the salary for this young but well-qualified man. They offered him £200 instead of the £375 that Staiger had received or the £700 that equivalent duties in Queensland commanded. By 14 December 1880, Haswell had resigned. In 1883 he was acting curator of the Australian Museum and in 1890 Professor of Zoology at the University of Sydney.

When Charles De Vis from the Museum in Manchester was appointed curator in February 1882, a surge in the Museum's work began. During his appointment, De Vis wrote 136 scientific papers and 120 articles in newspapers. He described 371 new species of vertebrates including 137 of fish, 107 of birds, 70 of reptiles, 14 of mammals and seven of frogs. He drove his staff hard, remaining in the Museum while they undertook the collecting. Kendall Broadbent, who was employed from 1882, collected vertebrates, molluscs and insects from Cardwell and Tully (1882), Charleville (1883), Cape York and the Gulf of Carpentaria (1883-4), Rockhampton (1888) and Bellenden Ker Range and Herberton (1889). The invertebrate, and in particular the insect, collections were curated by Henry Tryon, who also had to deal with clerical work. The insects had been looked after previously by Mrs Coxen. She went on a trip to England in 1883 after she had resigned and was asked to bring back some glass eyes for taxidermy. A major coup came when items collected under the direction of William MacGregor, Administrator and later Lieutenant-Governor of British New Guinea, found their way to De Vis. The specimens included 3,000 birds, amongst which were many new species.

This fortuitous influx of specimens was especially valuable as an economic depression led to the retrenchment of Tryon and five other members of staff in 1893. De Vis, Broadbent and an entomological curator were reduced in rank or salary and the three ran the Museum with the help of a clerk who was paid only six shillings a week. De Vis worked every day, including Sunday.

Long hours and hard work took their toll and, as was to be expected, tensions developed when small incidents assumed exaggerated importance. When a member of the public complained of an attendant's behaviour in the gallery, De Vis instructed the staff:

"Grave inconvenience have arisen from attendants while on duty in the public rooms allowing themselves to be drawn into conversation with, or volunteering information to visitors. They are instructed to refrain altogether from addressing visitors except in the maintenance of order. They are required to confine themselves to brief but courteous answers about exhibits and they are warned to be especially careful to avoid making to each other, within the hearing of visitors, remarks which may be misconstrued and complained of as offensive."

THE CHARACTER OF EARLY COLLECTIONS

The above quotation emphasizes the character of museums and their staff at this period. The scientific staff had a very thorough knowledge of taxonomy and the collections were displayed in a comprehensive and crowded manner. The public were expected to view the displays with the reverence due to the variety of complex patterns rather than to understand any aspect of biological interaction other than the basic dietary habits of carnivores and herbivores. Displays were rarely changed except to add new specimens. Practically the only means of keeping in touch with new display trends was by participation in international exhibitions.

Of the three other museums established in Australia in the 19th Century, the development of only the one in Hobart is comparable. The Western Australian Museum and the Queen Victoria Museum and Art Gallery in Launceston were founded in 1891, although the collecting had started a few years earlier.

In Hobart, collecting commenced by the Royal Society of Tasmania in 1839, but State support was not forthcoming until 1849. Thomas Roblin, the first curator, was appointed in 1862, a year before a purpose-built museum opened under the control of the Royal Society of Tasmania. The collections were poorly financed and exchanges made were one-sided. The appointment of Alexander Morton in 1884, an American who had worked for some time at the Australian Museum, led to a broadening of interest to include art, which is maintained to the present day. Morton's other important contribution was to place the emphasis on the display of Tasmanian exhibits.

The Museum in Hobart became a public institution in 1885. In the same year, the Royal Society's branch museum in Launceston was opened to the public, though it was given to the City Council in 1889.

The character of the early public collections in Australia was derived from a combination of quality of the staff and funding. Funds were more readily available in the 1860–65 and 1880–1888 periods than at other times. The Australian Museum and the private collectors led the way in initiating field trips, leaving other public museums to rely on exchanges and donations. Of the directors, McCoy in Melbourne reigned the longest and for a time had the best collection. His chosen location at the University jeopardized funds, however, and Krefft's field work and Macleay's exchanges eventually placed Sydney in a better position. When Macleay and Krefft fell out, Ramsay succeeded in maintaining the lead by judicious appointments to his staff. At about this time, Stirling in South Australia and De Vis in Queensland took firm control of collections that had run down or had remained in amateur hands.

Kohlstedt's (1983) excellent review of priorities and scientific initiatives of Australian museums of natural history in the 19th Century explains how museums were drawn into the bureaucracy of government by financial strings. It was essentially a three cornered battle for funds: the pursuit of collections and educational accountability representing the government; the staff and the public. In practice, the situation was complicated by the multiple positions occupied by men of influence such as trustees, by the need or desire of some staff to supplement their salaries by taking on private commissions and by political point scoring and expedient justifications.

Gaining Experience

The years through to 1940 were, to Australian museums, a period of maturation. A general shortage of funds was faced in different ways: the Australian Museum concentrated more on its staff (and had noticeable conflicts), the National Museum of Victoria managed to buy or otherwise acquired considerable collections, the South Australian Museum tried to do both and the Queensland Museum had little success with either. The fledgeling Western Australian Museum's natural history collections were presided over by a single person (L. Glauert) from 1910 until 1957 and in no way rivalled those of other States. Similarly, the museums in Launceston and Hobart were without the resources to make them serious competitors to those on the mainland.

The superior conditions at the Australian Museum, compared with other museums in Australia, began to wilt a little with the advent of World War I. Before the war, the staff fell

largely into two age groups, the young cadets and the mature scientists. The war influenced some of the former to leave and some of the latter retired or died. Wartime economies bit deeply into the available funds.

The situation was worsened by antipathy between the heads, Etheridge, and his deputy, Charles Hedley. When Etheridge died in 1919, Charles Anderson replaced him over the logical successor, Hedley. There followed a period of twenty years in which the scientists worked away at their pet projects while around them internal committees wrangled amid Public Service Board inspections. In the late twenties, an output of thirty or so scientific papers a year was maintained, although the standard of some was low. One particularly important publication was Musgrave's *Bibliography of Australian Entomology, 1775 to 1930*, published in 1932.

During this time, field expeditions were undertaken and the collections were augmented steadily. Insects and birds were the most numerous animals collected.

The National Museum of Victoria was fortunate to have a second long serving honorary director, W. Baldwin Spencer (1899 to 1928), and an able Curator of Zoological Collections, James Kershaw (1901 to 1931), but other scientific staff were almost non-existent. One of the Museum's strengths was its insect collection which Spencer claimed as the best in Australia. Certainly, with the saving of his salary, funds should have been available for other purposes, including the purchase of specimens (Table 9.11).

James Kershaw, Baldwin Spencer's second in command at the National Museum, succeeded Spencer in 1929, but being of nearly similar age, had to retire in 1931. David J. Mahony, a geologist, replaced him and immediately set out to encourage research. At that time, severe budgeting cuts ruled out the possibility of appointing new staff, but the following honorary biologists were appointed: J. Kershaw (Zoology), H.W. Davy (Entomology) and F.A. Cudmore (Palaeontology). The *Memoirs of the National Museum of Victoria* were revitalized. Funds became scarcer still and collections were bought by public subscription whenever possible.

The collections acquired by the National Museum (Table 9.11) and the South Australian Museum (Table 9.12) during the period 1900 to 1940 show the popular amateur collecting groups of beetles, butterflies, birds' eggs, shells and birds to be well represented. By comparison, the Queensland Museum acquired virtually no vertebrates during most of this period and the history of the entomological collections is chequered (Mather, in press). It was Director De Vis' wish that the entomology collections of the Queensland Museum be expanded. To this end, he offered his Sunday allowance to fund an insect collector, embarrassing the authorities sufficiently to employ an official collector, Charles Wild, in 1889. Unfortunately, Wild was interested principally in molluscs and during his 22 years with the Museum he achieved very little entomologically.

Wild rose to be Acting Director on De Vis' retirement in 1905, but was in trouble by 1907 when the trustees were disbanded, in part due to newspaper criticism of the effectiveness of the Museum displays, although the collections were praised. The Premier eventually asked Etheridge of the Australian Museum to come and report on what should be done. Etheridge was scathing about the general atmosphere and recommended the appointment of an experienced Director.

Hamlyn Harris was appointed in 1910. One of his first actions was to send Wild into the field to collect insects in the middle of winter, in which task he failed miserably, injured himself by falling over, became unwell, suffered bitter frost and accidentally set fire to his camp, destroying all his possessions.

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Table 9.11 Collections acquired by the National Museum of Victoria, 1900-1940.

DATE	ANIMAL	SPECIMEN	SPECIES	TYPES	COST	ORIGIN
1900	zebra	several			£30 each	R. Ward, London
1902	fossils	thousands			donation	G. Sweet
1902	mammals/birds/ reptiles				donation	Spencer and Gillen
1903	birds					J.W. Gregory
1904	Coleoptera	thousands			loan	G. Howitt
1913	Mollusca	500		co-types	donation	H.C. Dannevig
1915	birds eggs	1 884	591		donation	A.J. Campbell
1916	mammals/	480				
	reptiles	300		7		B. Spencer
1917	birds	8 547	714	67		H.L. White
1918	Coleoptera	4 119			purchase	C. French
1921	insects				donation	D. Gouldie
1921	Lepidoptera			14	donation	W.E. Elliot Drake
1923	Hydrozoa				donation	W.M. Bale
1923	Coleoptera				purchases	H.J. Carter
1927	birds eggs	13 000	840		bequest	H.L. White
1932	Lepidoptera	51 216	6 177	534	donation	G. Lyell
1933	ants	8 000	1 000+	some	purchase	J. Clark
1934	chitons	4 500	200	many	bequest	J.S. Mackay
1934	Thysanoptera		120	15	purchase	R. Kelly
1935	mollusca	35 000	7 300	40	purchase	J.H. Gatling
1937	fossils	thousands			donation	F.A. Cadmore
1940	Lepidoptera/	10 005	2 246			
	Coleoptera	12 100	5 200		purchase	W. Kershaw

Table 9.12 Acquisition of collections by the South Australian Museum during the period 1900-1940. (Data from H.M. Hale, 1956)

DATE	ANIMALS	SPECIMENS	COST	ORIGIN
1900	microlepidoptera	2 500	purchase	E. Guest
1902	land shells, vertebrates and insects	a great number	donation	R.T. Maurice
1902	molluscs		bequest	J. Phillips
1902	African mammals		donation	R.M. Hawker
1911	insects	45 000	purchase	T. Blackburn
1914	Antarctic birds	49	donation	D. Mawson
1918	beetles	thousands	purchase	A. Swinson
1918	butterflies	80 000	purchase	T.P. Lucas
1918	birds eggs	468 clutches	purchase	Kearland
1918	beetles and butterflies	5 000	collection and donation	Aitape and Madang
1918	birds		donation	A.J. Hunter
1922	insects/birds	7 000/164	collection	N.B. Tindale
1920's	insects	20 000	collection	H.M. Hale
1922	birds	112	donation	F.E. Parsons
1923	butterflies/birds	4 000/36	purchase	J.F.W. Schulz
1923	birds	379	purchase	F.M. Littler
1926	insects	10 000	collection	A.M. Lea
1926	molluscs		donation	J. Verco
1927	insects	70 000	purchase	O.B. Lower and others
1927	birds	300	donation	R.M. Hawker
1929	molluscs		purchase of 500	L. May
1930's	birds eggs	2 000 clutches	donation	J.N. McGillp
1932	beetles	50 000	purchase	A.M. Lea
1938	birds	1 972	purchase	W.D.K. McGillivray
1940	birds	1 066	purchase	F.E. Parsons

Wild was then dismissed by Harris and replaced by Henry Hacker who seemed tough and reliable, undertaking collection trips by bicycle, and later motorcycle, and publishing a number of papers. He was transferred to the Department of Agriculture in 1921, but still worked one or two days a week in the Museum until 1943. Just before he left he sold a large collection of Hemiptera, one of his favourite groups, to an American who later left his collection to the U.S. National Museum of Natural History. The suspiciously large gap in the Queensland Museum's collections was not noticed for many years.

Harris preceded the National Museum of Victoria by appointing honorary biologists in 1912. John Shirley was appointed as conchologist but after two years resigned, complaining of want of literature. He was reappointed for a year in 1920 (at age 71) in a paid position until he died in 1922.

Although Harris advocated the establishment of a marine station on the Barrier Reef, he was unable to obtain the necessary funds. In fact, Queensland remained in the doldrums, in spite of the efforts of several directors, until the trustees were reappointed in 1970.

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10. HUMAN EXPLOITATION OF AND INTRODUCTIONS TO THE AUSTRALIAN FAUNA

J. M. THOMSON, J. L. LONG & D. R. HORTON

ABORIGINAL EXPLOITATION OF THE AUSTRALIAN FAUNA - A MATTER OF CHOICE

Aborigines exploited a great range of Australian fauna, including certain invertebrates (arthropods, molluscs and echinoderms) and all the vertebrate groups, both for food and for the manufacture of artefacts. The general pattern of Aboriginal diet can be summarized as a concentration, varying with seasonal abundance, on a few staple items. These items were usually relatively small animals which could be either collected or hunted by a technique which enabled large catches and whose abundance was predictable because of some aspect of reproductive behaviour or aspects of habitat choice. In addition, there were usually a number of less frequently obtained items which were sought for particular reasons, but whose abundance was less or whose behaviour was less predictable.

This general pattern varied considerably depending on geography and divisions such as coastal inland, tropic/temperate, desertic/mesic, low altitude/high altitude and riverine/non-riverine can be recognized. Because the use of certain species as staples was dependent upon their availability and because most Aboriginal groups used mobility as part of their economic strategy, there tended to be little long-term effect of exploitation on animal species. Some exceptions to this will be examined below. In addition, Aboriginal use of fire certainly caused some environmental modification and this may have affected certain faunal elements. The only animal species known to have been introduced by Aborigines, the Dingo, probably had direct adverse effects on the native marsupial carnivores and indirect effects on other species.

Major Exploited Faunal Groups

Macropodids. Macropodids were probably the major group of animals exploited by Aborigines in Australia. Because of the variety of species involved, there was a considerable range of strategies of exploitation and consequent effects. A useful broad division of strategies is evident between those for large kangaroos and for small wallabies. Large species generally were hunted singly and such hunts had a low chance of success (Jones, 1980; Gould, 1980). The inclusion of kangaroos in mythologies and totemic systems and the resulting prohibitions also helped to reduce the impact of exploitation (Newsome, 1980). In addition, much of the burning carried out by Aborigines was done with the intention of providing improved grazing conditions (Hallam, 1975), although this would have been balanced to some extent because the patches of grass provided a focus for hunting activities (Jones, 1969).

Small wallabies tend to be more predictable in their occurrence, so more certain harvesting methods could be used. As a result, wallabies such as *Petrogale*, *Lagorchestes*, *Thylogale*, *Bettongia* and small *Macropus* were harvested in quite large numbers. Methods used included trapping and driving, the latter often with the use of fire to burn out a

patch of dense scrub. Such methods, and such levels of exploitation, are much more likely to have affected these species than was the solitary hunting of large kangaroos. The only positive evidence is some apparent extinctions of local populations of *Petrogale* at two northern Australian sites (Horton, 1981). Nevertheless, macropodids have been exploited for at least 30,000 years in Australia and there appear to be no examples of extinct species due to hunting among the smaller members of the family.

Possoms. Possums were hunted all over Australia. As well as being used for food, their skins were used for clothing in southern Australia (Wright, 1979) and possum fur string was made over much of the continent. The jaws were used as tools in some areas (Mulvaney, 1973). Possums were a very common item of diet, but the exploitation seems to have had a strong seasonal aspect and young, newly-independent animals, which would in any case have a high mortality rate, were probably the age group harvested most heavily (Vanderwal & Horton, 1984). There are records of their being smoked out of hollow trees.

Button Birds. Mutton birds were exploited at various stages during the breeding period. In November, birds washed ashore after storms were collected all down the southeastern coast (Gaughwin, 1978; Lampert 1971). On the Bass Strait islands and in Tasmania, eggs, together with adult birds, were harvested early in the season and young birds late in the season. This harvesting has been continued for several thousand years at least, with little apparent effect, possibly because the offshore nesting islands were only accessible in favourable weather conditions (Vanderwal & Horton 1984).

Seals. The harvesting of fur seals around southern Australia dates back at least 8,000 years (Jones, 1971), but appears to have had little effect. This was probably partly due to the inaccessibility of breeding grounds, but also because the main harvesting effort seems to have been concentrated on yearling seals, which had a low natural rate of survival (Vanderwal & Horton, 1984; Horton, 1979).

Fish. Fish were exploited extensively wherever available and frequently formed a major diet staple. As a consequence, there were major technological developments associated with fishing. The whole range of possible fishing practices, nets, hook and line, spears and traps of various kinds (tidal traps made from rocks, fences, conical basket traps and so on), were put to use. In some sites, there seems to be evidence for changes in species composition and size of fish harvested with changes in technology (Bowdler, 1970). The use of hook and line, for example, appears to be a relatively recent innovation dating back only one or two thousand years (Rowland, 1981). There appears to have been no serious impact on fish species, since fishing dates back at least 30,000 years and species obtained then are still extant (e.g. Kefous, 1977). Evidence for a positive impact in the case of eel species in Victoria exists in the form of extensive systems of

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ditches probably initiated several thousand years ago, which extended the range of eel species, allowing them access to rich swamps (Lourandos, 1980).

Insects. The main species exploited were bees (for honey) and some coleopteran and lepidopteran larvae and adults. The exploitation of the larvae would have had little effect although some were harvested in very large numbers (Kimber, 1984). Bogong Moth adults were harvested while they were hibernating in the Snowy Mountains, people apparently travelling to known sites and camping there specifically for the harvest (Flood, 1980). Such exploitation would seem likely to have an effect, but does not seem to have done so, perhaps because there were always inaccessible hibernating sites which provided refuges for some of the moth populations. The exploitation of bees involved the chopping of hives out of trees; such destructive harvesting may have affected some populations.

Molluscs. Evidence for human exploitation of shellfish in Australia extends back almost as far as the first known human occupation of the continent, some 35,000 years (see Bowler *et al.*, 1970). Wherever molluscs were available, including marine, freshwater and terrestrial species, they were utilized. As well as being used for food, the shells of a number of species were used as tools and ornaments. The value of some of them is indicated by the fact that they were traded across thousands of kilometres along trade routes extending, for example, from Cape York through to Lake Eyre (Mulvaney, 1975). Molluscs tend to produce a large amount of waste material (shell) in relation to the amount of food they contain. Above a certain critical level, the presence of shells provides a self-preserving (alkaline) environment. As a consequence of those two factors, shell middens are among the most common, most visible and often the most impressive prehistoric sites in Australia.

Because of this phenomenon, the importance of molluscs in the diet tends to be overestimated. Even in coastal areas they probably provided only some 25% of the diet. On the other hand, the occurrence of mollusc species was predictable, they were easy to gather and they provided high quality nutrition, so that their importance was considerably greater than is suggested by a simple weight proportion (Meehan, 1982).

The impact of human exploitation of mollusc populations is difficult to determine. Certainly, the archaeological record reveals considerable variation in exploitation of different species. Environmental conditions (even such ephemeral phenomena as storms) have major impacts on molluscs and changes in the environment seem likely to account for most changes in exploitation. There was size selection while gathering, so that young ones would not be taken, and probably selection by area. A site heavily exploited recently would not be worth another trip until the population had recovered. Particularly heavy gathering possibly may have caused local population extinctions, particularly when combined with environmental fluctuations.

Megafauna. Interest in the extinction of the megafauna, the giant relatives of modern fauna occurring on each continent until the end of the Pleistocene, has almost rivalled that of the equally mysterious extinction of the dinosaurs. One of the two main hypotheses for Australia would require mass kill sites of the kind seen in North America and Europe, where herds of animals were driven over cliffs or into enclosures to be slaughtered. There is no evidence for such kill sites in Australia nor, until recently, has there been more than equivocal evidence that megafauna were even exploited by humans. Indeed, the suggestion has been made that they were not exploited at all because the early colonizers of Australia were essentially littoral inhabitants with a diet of fish, shellfish and small mammals (Bowdler, 1977). That the extinction

occurred as a result of human modification of the environment by fire also has been suggested (Jones, 1968; Merrilees, 1968). Neither of these suggestions appears to be correct. The megafauna probably was exploited, but only occasionally and with rare success, much like the exploitation of the large kangaroos. That such exploitation could have had any major effect on the megafaunal species is inconceivable. Use of fire is unlikely to have caused extinctions because at most the effect could have been to improve conditions for the megafauna (Horton, 1984). The occasional successful buffalo hunt in the Northern Territory in recent times is probably a useful analogy.

Introductions

Dingo. The Dingo appears to have been the only species of animal introduced into Australia by Aborigines, some 3,000 years ago. This corresponds to a time when there seems to have been some major changes in Aboriginal society and technology, a correspondence which suggests that there may have been movement of people into Australia about this time or, at least, increasing trade contacts. When the Dingo was introduced, there were two large marsupial carnivores in Australia, *Thylacinus cynocephalus* and *Sarcophilus harrisii*. The fact that these two species survived in Tasmania (which the Dingo did not reach) has long been seen as a proof that dingoes caused their extinction (presumably through competition) on the mainland. The finding that the two marsupial species became extinct on the mainland some 3,000 years ago seemed to confirm this hypothesis. Recent work, however, suggests that these species survived on the mainland until much more recently. Further, it is difficult to conceive of the Dingo as a competitor for *Sarcophilus*. The extinctions possibly were coincidental and occurred in response to environmental change in the last four thousand years. That the Dingo had an effect seems likely, but a more subtle and gradual one than has been supposed. *Thylacinus* and *Sarcophilus* may have had an almost symbiotic relationship: *Thylacinus* essentially a hunter meat-eater, leaving carcasses with bones intact which could be scavenged by *Sarcophilus*. The Dingo may have made much more complete use of a kill, leaving little available for *Sarcophilus*. In addition, dingoes clearly had a radical effect on large fauna (kangaroos in particular), possibly because they make use of a broad spectrum of food items. *Thylacinus* may have had a more specialized relationship with large macropods. Extensive reduction of macropod numbers in an area by dingoes could have markedly affected their ability to obtain food. Such affects would be attritional rather than dramatic and we might expect them to have taken several thousand years to produce inviable mainland populations of *Thylacinus* and *Sarcophilus*.

Patterns of Exploitation

Several factors explain the most important central fact of Aboriginal exploitation of the Australian fauna: the almost complete lack of deleterious effect over some 40,000 years of exploitation. This astonishing achievement stands in stark contrast to the effects of European exploitation in just 200 years.

Aboriginal exploitation had a direct and limited purpose. It was designed to feed relatively small groups of people in a short time. There was almost no storage of animal foods and (perhaps as a consequence) almost no trade in animal food. People engaged in hunting or gathering were doing so to provide food for themselves and their kin that day, with perhaps some left over for the following day. There was no

purpose, then, in large-scale slaughter. By and large, the size of groups and territories were adjusted so that food was available through the year at a reasonable level.

Food seems to have been the primary consideration in hunting and gathering. Such materials as skins, bones and shells were taken from animals solely as by-products of the process of obtaining food.

Animal species were inextricably woven into Aboriginal religious life. Animals were not completely separate from humans, but were derived from the "Dreaming", as were humans. The place of animals in the cosmos, their rights and the obligations of humans to them were explicitly recognized. All Aboriginal groups had systems of prohibitions on killing animals, ranging from complete protection for some species to protection at certain times for others or prohibitions against certain people killing certain animals. Similarly, the landscape was an integral part of the cosmos. Certain places were "off limits" to certain people or certain activities were forbidden in some places. Those landscape prohibitions had the effect of protecting at least some animal species or at least of providing refuges for parts of populations.

Aboriginal technology was limited in its scope. While adequate for the direct and limited purpose of exploitation, it was not adequate to go beyond that. A hunter with a rifle, for example, can be almost sure of hitting and killing a kangaroo. The chances of success with a spear are much lower. A hunter with a truck can carry hundreds of kangaroo carcasses, a hunter on foot only one. People with large boats with motors can be sure of reaching an offshore seal colony in any season, people with low draught canoes cannot. People with freezers can obtain enough food for a whole summer in one hunting trip and keep it fresh for that long, but people without freezers need to acquire fresh meat each day. People with guns can slaughter a whole seal colony with impunity, but people without them avoid bull seals (and consequently females and newborn young) and hunt yearling seals. Finally, and perhaps most importantly, Aborigines exercised choice and had sufficient mobility to enable them to do so effectively. People in permanent settlements, when food is short, may well need to kill the last wild goat, take the last clutch of duck eggs or collect the last few oysters. People who are mobile are free to maintain a high standard of diet by exploiting mutton birds in autumn, wallabies in winter, possums in spring and seals in summer, making up for any shortfalls caused by weather conditions by exploiting alternatives, such as shellfish, bandicoots, snakes, lizards, frogs, fish and rodents. All of this animal food was underwritten by the use of plant food, which probably always comprised the bulk of the diet and was exploited according to a seasonal pattern. When and where resources are abundant they are exploited. When their numbers fall away as a result of that exploitation, the target and/or the locality is changed. There will be no point, and no need, to exploit that resource until it once more becomes abundant either as a result of seasonal or longer-term cycles. The fact that Aborigines had an abundance of choices of fauna to exploit was probably the greatest single factor in maintaining all elements of that fauna through 40,000 years of interaction.

Exploitation of and Introduction of Animals in Australia since the arrival of European Man

The impact of European man on the fauna and flora of Australia is generally believed to be far greater than that by Aboriginal man. The extent of the impact in the space of two hundred years can be gauged from the following review.

There is no doubt that over-exploitation and the introduction of exotic animals together have had a substantial effect on the present distribution and composition of the fauna.

Native species exploited and the origin and date(s) of introductions of exotic vertebrates has been included in Tables 10.1 and 10.2. The reintroductions and relocations of native mammals within Australia are contained in Table 10.3.

Exploitation refers to the utilization of animals by man, for food, skins, sport and other reasons. The animal may eat or destroy cultivated crops or livestock and be persecuted for this reason. Commercial exploitation is the harvesting of animals for profit or gain. Over-exploitation results in a reduced population and can lead to a particular species becoming threatened, endangered or, in extreme cases, to its complete extinction.

Indirect extermination of animals may result from the alteration and destruction of habitat by man as well as the effects of the introduction of exotic animal forms. Introduced species are those which are deliberately or accidentally released or have escaped into an area in which they do not occur naturally. Some introduced species become successfully naturalized and persist as wild populations. The term "exotic" is generally reserved for those species which have an origin other than in the country of introduction.

Exploitation of Native Vertebrates

The principal causes of species extinction are over-exploitation of populations and modification of their environment (Holloway, 1979). Habitat destruction affects the greater number of species, but exploitation is frequently a contributory cause.

In the early days of European settlement, many vertebrates were exploited by shooting and trapping for food and for their hides. The fur industry developed as the land was cleared and the first crops were planted. The harvesting of animals for their skins and later for pet-meat became a way of life for many Australians. Many animals also were destroyed because they conflicted with agricultural pursuits. This resulted in the wholesale destruction of some species, especially macropodids. Once the land was settled and the human population became well established, there was time to pursue the fauna for sport.

Attempts at commercialization of wild animals in Australia in the past for the fur trade, for example, have generally ended in disaster, both for the animal population involved and the industry (Frith, 1973). Where proper management is applied, however, several industries are now functioning without detriment to the animal populations.

Generally, the effects of exploitation are difficult to separate from other factors, such as the effects of clearing for agriculture and the grazing of domestic stock. In the 1950's and 1960's, a world-wide boom in the demand for caged birds reached astronomical proportions. Species of Australian finches, parrots, lorikeets and cockatoos were heavily trapped for the overseas market. The legal export trade was stopped by government-imposed bans in 1960. Nevertheless, illegal trafficking in birds continues.

Mammals. Many native mammals were exploited either as food, for their fur, for sport or as pests in Australia. The Platypus, *Ornithorhynchus anatinus*, was trapped in early times because of its rarity. Its skin was also valuable as a curiosity for sale to overseas buyers (Troughton, 1967).

Shortly after the colony was founded, convicts in Tasmania killed and ate Tasmanian Devil *Sarcophilus harrisii*. In the 19th Century, settlers cooked and ate wombats, *Vombatus*

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Table 10.1 Commonly exploited vertebrates.

SPECIES	REASON	PRESENT STATUS
(a) MAMMALS		
<i>Ornithorhynchus anatinus</i>	skins	common
<i>Sarcophilus harrisii</i>	food, pest	common
<i>Macrotis lagotis</i>	skins, sport	rare, range reduced
<i>Macrotis leucura</i>	skins	rare, or extinct
<i>Phascalarctos cinereus</i>	skins	common, range reduced
<i>Vombatus ursinus</i>	food, sport, pest	common
<i>Pseudochirus peregrinus</i>	skins	common
<i>Trichosurus vulpecula</i>	skins	abundant
<i>Trichosurus caninus</i>	skins	common
<i>Bettongia penicillata</i>	sport, pest	rare
<i>Bettongia lesueur</i>	pest	extinct on mainland
<i>Petrogale xanthopus</i>	skins	fairly common, range reduced
<i>Thylogale billardierii</i>	skins, food	abundant, range reduced
<i>Thylogale thetis</i>	food	common
<i>Macropus eugenii</i>	sport, pest	common, limited
<i>Macropus greyi</i>	skins, sport	presumed extinct
<i>Macropus irma</i>	sport	common
<i>Macropus rufogriseus</i>	skins, food	common
<i>Macropus parryi</i>	skins	common
<i>Macropus giganteus</i>	sport, skins	abundant
<i>Macropus fuliginosus</i>	skins, food, sport	abundant
<i>Macropus robustus</i>	sport, pest	abundant
<i>Macropus antilopinus</i>	sport	common
<i>Macropus rufus</i>	skins, food, sport, pest	abundant
<i>Wallabia bicolor</i>	skins	common
<i>Setonix brachyurus</i>	food, sport	common, range reduced
<i>Onychogalea lunata</i>	? pest	presumed extinct
<i>Thylacinus cynocephalus</i>	skins, pest	extinct
<i>Hydromys chrysogaster</i>	skins, pest	sparse to common
<i>Arctocephalus pusillus</i>	skins	abundant
<i>Mirounga leonina</i>	blubber, oil	abundant
(b) BIRDS		
<i>Entomyzon cyanotis</i>	sport	common
<i>Philemon corniculatus</i>	sport	common
<i>Anthochaera carunculata</i>	sport	common
<i>Ptilonorhynchus paradoxus</i>	sport	fairly common
<i>Ptilonorhynchus violaceus</i>	sport	common
<i>Oriolus sagittatus</i>	sport	common
<i>Ailuroedus crassirostris</i>	sport	fairly common
<i>Sericulus chrysocephalus</i>	sport	fairly common
<i>Sphecotheres viridis</i>	sport	common
<i>Trichoglossus haematocephalus</i>	sport	common
<i>Trichoglossus chlorolepidotus</i>	sport	common
<i>Barnardius zonarius</i>	farm pet meat	common
<i>Coturnix ypsilophora</i>	sport	common
<i>Coturnix pectoralis</i>	sport	common
<i>Leipoa ocellata</i>	sport	fairly common
<i>Megapodius reinwardt</i>	sport	fairly common
<i>Alectura lathami</i>	sport, food	common
<i>Ardeotis koni</i>	food, sport	fairly common
<i>Dromaius novaehollandiae</i>	pest, sport, eggs	common
<i>Dromaius minor</i>	food	extinct
<i>Morus serrator</i>	fish bait	fairly common
Anatidae	sport, food	most species common
<i>Biziura lobata</i>	food	common
<i>Puffinus tenuirostris</i>	food, oil, down	common
<i>Cereopsis novaehollandiae</i>	food	common
<i>Phaps spp.</i>	sport, food	common
<i>Leucosarcia melanoleuca</i>	sport	common, range reduced
(c) REPTILES		
<i>Crocodylus johnstoni</i>	skins	common
<i>Crocodylus porosus</i>	skins	abundant
<i>Eretmochelys imbricata</i>	shell	endangered
<i>Chelonia mydas</i>	shell	declining

ursinus, on King Island (see Table 10.1 for other species). The hunting of most of the smaller wallabies (*Bettongia*, *Petrogale*, *Wallabia* and *Thylogale* spp.) and larger kangaroos (*Macropus* spp.) was considered good sport. In about

1904, dealers in Adelaide traded *Bettongia penicillata* for ninepence a head for coursing. The pelts of *Macrotis* spp. were being sold in 1923 (Troughton, 1967).

Table 10.2 Vertebrates introduced and established in Australia.

SPECIES	ORIGIN	DATE(S) INTRODUCED
MAMMALS		
(a) Deliberate Introductions		
<i>Oryctolagus cuniculus</i>	Europe	1859
<i>Lepus capensis</i>	Europe	before 1862
<i>Vulpes vulpes</i>	Europe	1845-1854
<i>Cervus unicolor</i>	SE Asia	1863-1872
<i>Axis axis</i>	India	1862-1900
<i>Cervus elaphus</i>	Europe	1860-1918
<i>Cervus timorensis</i>	SE Asia	1868-1912
<i>Dama dama</i>	Eurasia	1829-1906
<i>Axis porcinus</i>	-	1866
<i>Antilope cervicapra</i>	India	1900
<i>Funambulus pennanti</i>	India	1898
(b) Accidental Introduction		
<i>Rattus rattus</i>	Eurasia	1788
<i>Rattus norvegicus</i>	Eurasia	1788
<i>Mus musculus</i>	Eurasia	1788
(c) Feral Mammals		
<i>Equus caballus</i>	domestication	1788→
<i>Equus asinus</i>	domestication	with settlement
<i>Capra hircus</i>	domestication	with settlement
<i>Bos taurus</i>	domestication	1788
<i>Bos javanicus</i>	domestication	1829-1840
<i>Bubalus bubalis</i>	domestication	1825-1886
<i>Sus scrofa</i>	domestication	with settlement
<i>Camelus dromedarius</i>	domestication	1840-1920's
<i>Felis catus</i>	domestication	1840-1920's
BIRDS		
(a) Deliberate Introduction		
<i>Passer domesticus</i>	Europe	1863→
<i>Passer montanus</i>	Europe	1863→
<i>Sturnus vulgaris</i>	Europe	1859-1880
<i>Acridotheres tristis</i>	Asia	1862-1883
<i>Turdus merula</i>	Europe	1857-1872
<i>Turdus philomelos</i>	Europe	1860-1870
<i>Alauda arvensis</i>	Europe	1854-1872
<i>Carduelis carduelis</i>	Europe	1860-1880's
<i>Carduelis chloris</i>	Europe	1860-1880's
<i>Anas platyrhynchos</i>	Europe	1871-1900
<i>Cygnus olor</i>	Europe	1897-1912
<i>Lophortyx californicus</i>	North America	1930
<i>Phasianus colchicus</i>	Eurasia	1920's
<i>Streptopelia senegalensis</i>	Asia	1898-1912
<i>Streptopelia chinensis</i>	Asia	1860-1912
<i>Pycnonotus jocosus</i>	Asia	1880
(b) Accidental Introductions (escapes)		
<i>Lonchura punctulata</i>	Asia	1930's→
(c) Feral Birds		
<i>Columba livia</i>	domestication	with settlement
<i>Struthio camelus</i>	domestication	after 1920's
<i>Pavo cristatus</i>	semi-domestication	occasional
<i>Gallus gallus</i>	domestication	occasional
<i>Meleagris gallopavo</i>	domestication	occasional
REPTILES		
<i>Hemidactylus frenatus</i>	Pacific Islands	since 1900
AMPHIBIANS		
<i>Bufo marinus</i>	Hawaiian Islands	1935-1937
FISH		
<i>Cyprinus carpio</i>	Europe	1870→
<i>Perca fluviatilis</i>	Europe	1862-1868→
<i>Salmo gairdneri</i>	Europe and North America	1864→
<i>Salmo trutta</i>	Europe and North America	1864→
<i>Salvelinus fontinalis</i>	Eurasia	1890's
<i>Carassius carassius</i>	Eurasia	1890's
<i>Carassius auratus</i>	Europe	1890's
<i>Tinca tinca</i>	Europe	1890's?
<i>Rutilus rutilus</i>	Europe	1890's?
<i>Gambusia affinis</i>	North America	1925-1935
<i>Xiphophorus helleri</i>	Asia	1960's or 70's
<i>Xiphophorus maculatus</i>	Asia	1960's or 70's
<i>Poecilia reticulata</i>	Asia	1960's or 70's
<i>Poecilia latipinna</i>	Asia	1960's or 70's
<i>Puntius conchonius</i>	Asia	1960's or 70's
<i>Acanthogobius flavimanus</i>	Japan	1971
<i>Tridentiger trigonocephalus</i>	Japan	1973

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By far the greatest exploitation for fur in Australia involved the fur seal *Arctocephalus pusillus*, Koala *Phascolarctos cinereus* and possum *Trichosurus vulpecula*. All were subjected to commercial exploitation on a scale sufficient to bring them close to extinction.

Concern for the diminution of numbers of *Phascolarctos* due to trapping was expressed as early as 1900 (Winter, 1979). Trapping, however, continued on a large scale. In 1908, 57,933 pelts passed through the Sydney markets. This total increased until in 1924 about two million skins were exported. Most harvesting was stopped by 1927, but continued in Queensland. Here, over half a million were trapped in that year.

Evidence suggests that numbers of *Phascolarctos* increased following European settlement. Towards the end of the 19th Century, however, a drastic decline in abundance occurred. By 1920, there were none in South Australia (Jones, 1923-25) and their range in Victoria was reduced considerably (Warneke, 1978). The decline in Queensland took place after 1927 (Gordon & McGreevey, 1978).

Commercial hunting was a factor in the decline of *Phascolarctos*, but so were epidemics of ophthalmic disease and pneumonia; severe bush fires also contributed to the decline (Frith, 1973; Warneke, 1978; Gordon & McGreevey, 1978). The result was that the species was eliminated from most of its range. With protection and re-introductions, however, they were restored to many areas. Populations of *P. cinereus* have now increased to levels where there is less likelihood of extinction.

The economic value of the fur of *Trichosurus vulpecula* was well known abroad in the period 1900-1935. In 1906, over four million skins were marketed in London and New York. Protection in the 1920's by way of "open seasons" restricted the trapping and hunting pressure. Exploitation continued, however, on a large scale. In 1926, an open season in two districts of New South Wales for fourteen days yielded 11,701 skins. Over one million skins were exported from that State in the 1931-32 season.

Trichosurus vulpecula was almost eliminated from much of its range. Unlike *Phascolarctos cinereus*, however, populations increased and recovered substantially under protection alone. The sale of the skins of *P. cinereus* is now completely banned. Exploitation of *T. vulpecula* continues in Tasmania (Winter, 1979). There, seasons are declared depending on the abundance of the animal.

Before the 1920's, there was some trade in the skins of another possum, *Pseudochirus peregrinus*. The last open season was held in Victoria in 1959 when 2,500 skins were marketed. During the peak harvest period in 1929-1938 some 3,975,700 skins were sold. Diminution of the trade was believed to be due to either poor skin quality (Ride, 1970) or to a decrease in the animal's abundance (Frith, 1973). *Trichosurus caninus* also was hunted for its fur in recent times. The last open season occurred in Victoria in 1963 (Winter, 1979). In a two month season, 90,295 possum skins were sold, many of which were from this species.

The fur of the Water Rat, *Hydromys chrysogaster*, was in demand in the 1920's and 1930's. It was trapped extensively both for this reason and the fact that some landholders considered it a pest. In open seasons which occurred infrequently in Victoria in the 1950's and 1960's, as many as 18,159 skins were taken in any one season. Exploitation was considered to be the cause of the collapse of the Tasmanian population (Guiler, 1957).

Many skins of wallabies and kangaroos have found their way into the fur trade (see Table 10.1). The expansion of grassland and provision of water for domestic stock in inland areas allowed large increases in the populations of some

macropodids. Large numbers were shot as pests of crops and pasture. *Bettongia penicillata* ate and trampled the crops of early settlers and many were trapped or poisoned.

The trade in kangaroos in recent times has been supported mainly by *Macropus rufus*, *M. giganteus*, *M. fuliginosus* and *M. robustus*. When the pet-meat industry commenced, the number of animals being shot rose considerably. In 1964-65, nearly five million kilograms of meat and one and a half million skins were exported. In Queensland alone, over one million kangaroos and wallabies were harvested (Roff & Kirkpatrick, 1962; 1966). The present export trade is about 102,000 kg of meat to France and the Federal Republic of Germany. The trade in skins and kangaroo products is worth about \$10 million, annually.

Management for kangaroos was introduced in all Australian states in the 1970's. The maintenance of substantial and secure populations of all the species is the foremost objective. By the commercial harvesting of kangaroos, the program ensures that their numbers are not excessive in areas used by both livestock and kangaroos.

Birds. Harvesting of the shearwater *Puffinus tenuirostris* began before the establishment of the first settlement at Sydney. Sealers living on the small islands in Bass Strait utilized the eggs and young for food. A locally important industry was started in which the young were salted, then frozen and sold as a delicacy. By-products such as oil and the down were also used. The oil was said to have medicinal properties.

This industry survives to the present day, but is closely monitored. Licensed operators harvest half a million chicks each year in Bass Strait. Despite the exploitation, some colonies are enlarging and occupying new sites (Naarding, 1981). On the Bass Strait islands the population numbers 15 to 16 million birds.

During the period 1797 to 1820, considerable exploitation of the Cape Barren Goose *Cereopsis novaehollandiae* occurred by sealers. The later resident human population continued to hunt them (Frith, 1967). More recently, several *C. novaehollandiae* were held in captivity to test the commercial prospects of the bird (Morrison, 1981).

Before the turn of the century, the Musk Duck *Biziura lobata* was netted, salted, smoked and eaten for food. This local Western Australia industry ceased in 1898 (Serventy & Whittell, 1967). The Dwarf Emu, *Dromaius minor*, became extinct due mainly to its slaughter by early settlers who ate the flesh. Fishermen reduced the gannet *Morus serrator* colony on Cat Island, Tasmania, by using the birds as bait for cray pots. The colony of 2,500 was reduced to 50 by 1952 (Carrick & Costin, 1959).

Many species of birds in Australia have been hunted for sport. Several quails and pigeons were considered game in early settlement days (see Table 10.1). Some, such as the pigeons *Leucosarcia melanoleuca* and bronzewings *Phaps* spp., were hunted in large numbers and became relatively scarce (Frith, 1973). They have increased in numbers with protection. Until 1945, several honeyeaters and other species (see Table 10.1) were acceptable game birds (Frith, 1973). Several other species were shot on a casual basis. For most, shooting was probably not a significant factor in their survival.

Waterfowl (Anatidae) are now the most important game-birds. Most species within the family are involved. Erratic breeding and movement patterns leading to vast fluctuations in numbers makes management difficult (Frith, 1973). The exploitation is now governed by the monitoring of populations and water-levels. These factors determine the timing and length of the open seasons.

Introduction of Vertebrates

Mammals

Deliberate Introductions. The population of the Rabbit *Oryctolagus cuniculus* in Australia originated from individuals imported and liberated on a grazing property near Geelong, Victoria and several other localities (see Chapter 45, this Volume).

Colonization was rapid and accomplished at the rate of >100 km/year. There is evidence accumulating, however, that any natural spread was assisted by a wide range of releases (Edmonds *et al.*, 1981). In 60 years they had spread to inhabit an area of 4,000,000 km² (Myers, 1983). The species now occupies most of Australia except the tropical north.

The spectacular success of *Oryctolagus cuniculus* in Australia may be related to the fact that many natural predators and parasites were not introduced (Dunsmore, 1981). There is no doubt that the consequences of the success were both widespread and serious (Myers & Poole, 1963; Cochrane & McDonald, 1966; Farrington & Mitchell, 1971). The grazing pressure in agricultural areas reduced domestic stocking capacity (Ratcliffe, 1959). The effect on native vegetation was responsible in part for the rarity of some native herbivorous species (Marlow, 1958).

With the introduction in 1950–51 of myxomatosis, a viral disease to which *Oryctolagus cuniculus* showed extreme susceptibility (Fenner *et al.*, 1957), their numbers declined. After three years the population in southeastern Australia was reduced by 80 to 90% (Frith, 1973). The use of 1080 poison since the 1950's has further reduced populations in Australia.

The Brown Hare *Lepus capensis* is also established in Australia. Some were established at Westernport Bay, Victoria by 1862 (Rolls, 1969). Hares established on Phillip Island in 1863 were widely distributed in the 1870's (Frith, 1973). The species is now found over a wide area of southeastern Australia (Mahood, 1983a).

Lepus capensis is a pest of some crops such as cereals and lucerne. In fruit growing areas they cause damage by gnawing the bark of fruit trees (Douglas, 1972). The species is a less significant pest than *Oryctolagus cuniculus*.

The Fox *Vulpes vulpes* became established in Australia from releases in 1845 (Rolls, 1969) and at later dates (Frith, 1973) in Victoria and elsewhere. It has also spread rapidly and is now distributed over most of the continent south of the tropics (Coman, 1983). It has not settled permanently in the far north of Western Australia (King & Smith, 1985).

The effects of predation by *Vulpes vulpes* on native wildlife and domestic stock is obscure for lack of sufficient data. Studies suggest that they are not a serious predator of lambs (McIntosh, 1963; Rowley, 1970). *Vulpes vulpes* has attributes which make it a danger to ground living native mammals which are adjusted to less efficient, adaptable and abundant predators (Marlow, 1958). Recent food studies (Coman, 1973; Seebeck, 1978) suggest predation of native species is greater in undisturbed habitats. Studies on *Bettongia penicillata* released in southwestern Australia indicate that *V. vulpes* can be a significant predator (Christensen, 1980).

Attempts have been made to establish at least 14 species of deer (Cervidae) in Australia. Of these, six are now established (Rolls, 1969; Bentley, 1978). *Cervus unicolor* is established in Victoria and the Northern Territory (Bentley, 1978). *Axis axis* was released numerous times without much success (Bentley, 1978). The most successful introduction was near Charters Towers, Queensland in 1886 (Roff, 1960) where the

species is still well established (Mitchell *et al.*, 1982). *Cervus porcinus* was released at Cape Liptrap, Wilson's Promontory and there are now small populations on the coast and offshore islands in this vicinity (Bentley, 1983). Several scattered populations of *C. elaphus* exist in Australia from introductions made up until 1918 (Roff, 1960; Rolls, 1969; Bentley, 1978). Those released in the Brisbane Valley area of Queensland in 1873–74 (Roff, 1960) have increased in numbers and range. The population now numbers 8,000 to 10,000 head (Searle & Parker, 1982). Colonies of *Cervus timorensis* exists in the Sydney area, on Prince of Wales Island and on Friday Island (Bentley, 1983). *Dama dama* is well established in Tasmania where it was introduced in 1850 (Wapstra, 1973) and is common in the Pikedale area of Queensland (Searle, 1980).

Generally, deer have not caused many pest problems in Australia. They have become numerous in the past, however, in some areas of Victoria (Frith, 1973) and Queensland (Searle, 1980) where they were destroyed to prevent damage to crops.

The Palm Squirrel, *Funambulus pennanti*, was released in the grounds of the Zoological Gardens, South Perth, Western Australia in 1898 (Long, 1972). In the last decade or two, this species has spread into some adjacent areas.

Accidental Introductions. Originally confined to the Oriental Region and central Asia, the rats *Rattus rattus* and *R. norvegicus* and the House Mouse *Mus musculus* have invaded the western world. All three are established in Australia. *Mus musculus* is now widespread even in remote desert localities. *Rattus rattus* occurs widely around the coastal fringe of the mainland and in Tasmania. *Rattus norvegicus* is abundant in larger cities and heavily developed areas near the coast (Watts & Aslin, 1981).

Periodically, spectacular eruptions of *Mus musculus* cause damage in grain growing areas and to pastures. *Mus* and *Rattus* spp. are severe pests of stored products and are considerable household pests. They are capable of transmitting several diseases to man. Though conceivable, there is no direct evidence that they have had some effect on populations of native rats and mice and some birds (Watts & Aslin, 1981).

Feral Mammals. Most of the domestic mammals widely used as stock in Australia now have feral populations in the wild. These colonies are the results of abandonment of stock, escape from captivity or the deliberate release of animals for sport.

Feral horses *Equus caballus* are known from the early days of European settlement. Some were feral near Sydney in the 1830's (Anon, 1977a). Descendants of the Timor Pony, abandoned in 1838, still roam the Cobourg Peninsula, Northern Territory (Letts, 1964). From 1918 to 1939, many horses were raised in western Queensland and the Northern Territory for use by military forces in India (Frith, 1973). Many of these were released or allowed to roam when increasing mechanization made horse breeding unprofitable.

At present, the most numerous herds of *Equus caballus* are in the north and northwest regions of Queensland (Mitchell *et al.*, 1982) and in the larger areas of undeveloped country in the north of the continent. In large numbers, they are a pastoral pest, destroying fences, fouling water points and competing with stock for pasture.

Derived from the wild ass of Asia, the Donkey *Equus asinus* was widely used as a pack and draught animal in early settlement times. Large teams hauled wagons and packs to inland centres. Particular use was made of them in the gold mining industry, on pastoral leases and in large construction projects. As the importance of these industries declined and

10. EXPLOITATION AND INTRODUCTIONS

motor transport improved, many donkeys were abandoned. As a result, they became established over large areas of northern Australia.

Population estimates in the Kimberley region, Western Australia in 1978 suggested that between 500,000 and 1,000,000 were present. Variation in the colour patterns of *Equus asinus* suggest the Australian population is made up of a number of different breeds (McCool *et al.*, 1981).

Equus asinus competes with domestic stock for food and water in some of our most arid environments. No research on the impact of the species on the ecosystems it now occupies has been carried out in Australia.

In the 19th Century, the common practice was to leave goats *Capra hircus* on offshore islands where they might assist shipwrecked mariners seeking food. Colonies have existed on a number of islands off the Australian coast (Kikkawa & Boles, 1976). Fortunately, on most they have either died out or been removed.

The feral populations now present on the mainland are derived from domestic animals which were abandoned, have escaped or were released by early settlers, miners and construction gangs (Letts, 1964; Long, 1972; Holst, 1981). *Capra hircus* now occurs in many areas in Australia, but mainly in the north. As many as 50,000 may be in Queensland alone (Mitchell *et al.*, 1982). There are possibly 200,000 to 350,000 in Australia (McKnight, 1976).

Research is in progress in several areas of Australia to determine the effects of *Capra hircus* in the environment. They are thought to compete with native fauna for food, shelter and water, particularly in semi-desert areas (Mahood, 1983b).

Feral cattle *Bos taurus* occur in some areas of Australia. It is difficult in most areas to determine which are feral and which are not. Stock brought in with the First Fleet wandered off and founded a small wild herd near Sydney in 1806 (Frith, 1973).

Another cattle species, the Banteng *Bos javanicus*, also is established. These animals were imported to Raffles Bay and Port Essington on the Cobourg Peninsula (Letts, 1964) where they became feral when the settlements were abandoned. They have slowly spread to occupy the whole peninsula.

Bos javanicus, together with the Water Buffalo *Bubalus bubalis*, are responsible for the introduction of the Buffalo Fly and the Cattle Tick to Australia (Ford & Tulloch, 1982).

Individuals of *Bubalus bubalis* were introduced to the military settlement at Fort Dundas on Melville Island in 1825 (Ford & Tulloch, 1982). Others were introduced to settlements at Raffles Bay in 1827-29, Port Essington in 1838-49, Victoria settlements in the 1840's and to Darwin in 1886 (Letts, 1964; Tulloch, 1969). Many of these animals were abandoned when the settlements were closed. Since then, they have spread widely on the sub-coastal plains and river basins between Darwin and Arnhem Land.

Bubalus bubalis has caused the decline of pasture productivity by overgrazing near waterways, trampling and by causing soil erosion and salinity problems. They are not compatible with areas set aside for the conservation of indigenous fauna and flora (Stocker, 1971; Ford & Tulloch, 1982; Williams & Ridpath, 1982).

Descendants of domestic pigs, *Sus scrofa*, are now established over wide areas of Australia. The largest populations are present in New South Wales and Queensland, but they occur in most States. Numbers within established populations fluctuate markedly, but increase rapidly in response to good

conditions (Pavlov, 1983). Density commonly reaches 60 to 80/km² (Anon, 1977a) and the total numbers of pigs in Australia may be as high as 975,000 (McKnight, 1976).

Besides causing damage to crops, *Sus scrofa* is considered to be a significant potential pest because of the role it may play in the dissemination of exotic diseases (Anon, 1977; Pavlov, 1983).

The One-humped Camel, *Camelus dromedarius*, was imported to Australia during early settlement for exploration and the transport of goods for pastoral and construction projects. Most of these animals were imported from India and the Middle East. Some 20,000 domestic camels were present in Australia in the 1920's.

As motor vehicles superseded *Camelus dromedarius* as a carrier, many were released or abandoned. Feral individuals now occur generally in central Australia in a variety of habitats. They prefer the sandy ridge-dunes of central and central-western Australia (Newman, 1983). Estimates of their numbers suggest that there may be 15,000 to 20,000 head (McKnight, 1976).

The impact of *Camelus dromedarius* on the fauna and flora has not been determined. They occasionally damage fences and watering places (Long, 1972; Anon, 1977).

The Domestic Cat, *Felis catus*, was introduced to Australia with the early settlers. They soon strayed and became feral. Some deliberate introductions were made in the hope they they might control rabbit numbers.

The effect of *Felis catus* as a predator on, or competitor of, native fauna is difficult to assess (Jones, 1983). They are blamed for contributing to the decline of a number of birds and small mammal species.

Birds

Well Established Species. The first release of the House Sparrow *Passer domesticus* occurred in 1863 in Victoria. In the next ten years, many other liberations occurred in various parts of eastern Australia (Long, 1981). *Passer domesticus* is now spread over much of the eastern half of Australia. Rates of spread from 6.7 km/year to 103.6 km/year are recorded (Blakers *et al.*, 1984). In suburban areas, density of birds can be from 33.7 to 39.1 birds per hectare (Jones, 1981; 1983).

A second sparrow species, *Passer montanus* is also established in eastern Australia (Sage, 1956). Introduced and released at the same times as *P. domesticus*, it has not had the same level of success. It has a considerably smaller range in southeastern Australia and has spread at a slower rate (Hobbs, 1957). In some towns near the Murray River, it outnumbers *P. domesticus*. Suburban densities as high as 29.2 birds per hectare are recorded (Jones, 1981).

Passer domesticus is largely a nuisance species causing minor damage to wheat, fruit and garden crops. It contributes to the defacement and deterioration of buildings by excrement and the blocking of downpipes with nesting materials. *Passer montanus* has caused few problems in Australia (Long, 1981).

Two members of the starling family (Sturnidae) are established in Australia. *Sturnus vulgaris* is widespread in eastern Australia. *Sturnus vulgaris* was released near Melbourne in the late 1850's, Hobart in 1860, Brisbane in 1869-70, Sydney in 1880 and Adelaide in 1881 (Long, 1981). It has spread largely in association with settlement and at the rate of 20 to 25 km/year (Blakers *et al.*, 1984). Density of birds varies from 0.31 in partly cleared grazed woodland (Ford & Bell,

1981) to 2.5 birds per hectare in irrigated fruit growing areas (Thomas, 1957). Communal roosts to 25,000 birds are formed (Wall, 1973).

Acridotheres tristis (the Common Mynah) is restricted to areas along the eastern seaboard. *Acridotheres* was released in Melbourne, Victoria in 1862 (Jenkins, 1977). Several other releases occurred between 1862 and 1872 (Long, 1981). In 1883, birds captured in Melbourne were released in Queensland to control locusts (Chisholm, 1919) and cane beetles (Hone, 1978). The species now occupies four areas along the eastern coast (Melbourne, Sydney, Toowoomba, Cairns-Townsville) which are rapidly becoming linked by further spread.

Two closely allied species (family Turdidae) also are established in southeastern Australia. The Blackbird *Turdus merula* is now widespread from liberations between 1857 and 1872 (Balmford, 1978) and its range is still expanding (Blakers *et al.*, 1984). The Song Thrush *Turdus philomelos* has increased little in range from releases in the same period. It became firmly established in the gardens and parks of Melbourne (Tarr, 1950) where it has remained with little outward spread in the last 100 years.

In their native ranges, both *Turdus merula* and *T. philomelos* cause some damage to fruits. *Turdus merula* is a pest of fruits in Australia, particularly to cherries in Tasmania (Long, 1981). *Turdus philomelos* is not sufficiently abundant to have caused any problems.

The Skylark *Alauda arvensis* was liberated in Melbourne in 1854 (Balmford, 1978), in Adelaide in 1862, Sydney in 1866, Queensland in 1869 and in Tasmania in 1862 or 1872 (Long, 1981). Its spread has been slow (Blakers *et al.*, 1984). It inhabits disturbed areas and has the potential to expand its range further. In Australia, it has caused damage to oil poppy seedlings (Blakers *et al.*, 1984).

Of several pigeons and doves (Columbidae) released in Australia, only three have become established. Feral pigeons *Columba livia* are present in all the cities, larger towns, and often remote towns, throughout Australia. The largest concentrations occur in urban and suburban environments where there are unlimited nesting places on the façades of older buildings. Food sources such as parks or grain terminals are usually not far away.

The turtle-doves *Streptopelia chinensis* and *S. senegalensis* are both established from releases in the late 1800's, the latter from liberations in the Zoological Gardens, Perth, Western Australia (Serventy & Whittell, 1967). The former was released in Victoria in the 1860's (Balmford, 1978), in Adelaide in 1881 (Boehmn, 1961), in Perth in 1898 (Sedgewick, 1958), Sydney in 1898 (Blakers *et al.*, 1984) and in Brisbane in 1912 (Lavery, 1974).

Columba livia became a significant pest in Queensland where intensive animal production was based on rations high in grain (Morris, 1969). The most serious damage, however, occurs in cities and towns where their excreta accumulates and fouls building structures. Large populations provide a reservoir for disease, some of which can affect man (Long, 1981). *Streptopelia chinensis* and *S. senegalensis* are nuisance species which sometimes eat poultry food, vegetable seedlings and, occasionally, other seedlings in nurseries.

The Asian Red-whiskered Bulbul, *Pyconotus jocosus*, is well established in Australia, but with a restricted distribution. It was first released in Sydney in 1880 and is well established there. A second population, possibly derived from escapees, has existed at Coffs Harbour since 1972 (Morris *et al.*, 1981). *Pyconotus jocosus* causes some damage to fruit and vegetable crops. At present, it inhabits mainly gardens and parks in urban areas.

Two cardueline finches (Fringillidae), *Carduelis carduelis* and *C. chloris*, and an estrildine finch (Estrildidae), *Lonchura punctulata*, are the survivors of numerous finch-like birds released largely between 1860 and 1880.

The Goldfinch *Carduelis carduelis* now ranges over much of southeastern Australia and Tasmania. A small population in Western Australia flourished until a sudden decline about 1970 caused them to become rare. The Greenfinch *Carduelis chloris* has not spread so widely as *C. carduelis*, occupying only the southern parts of southeastern Australia and Tasmania. The Nutmeg Mannikin *Lonchura punctulata* inhabits much of the eastern seaboard, from Sydney north to Cairns. The present populations of this species were derived from a series of escapes and releases since 1930. Their spread has been rapid, at least in some areas (Blakers *et al.*, 1984).

Carduelis carduelis and *C. chloris* are relatively innocuous species in Australia. *Lonchura punctulata* has the potential to displace native finch species (Immelman, 1960), but opinion differs as to whether this has happened (Frith, 1979; Immelman, 1982). It is a potential pest of rice crops (Long, 1981).

The first recorded releases of the Mallard, *Anas platyrhynchos*, were in 1871 and 1872 in Melbourne (Ryan, 1906). Other releases occurred at later dates in various States. The species is now well established in the southeastern portion of Australia. The main expansion in range has occurred since 1950 (Blakers *et al.*, 1984).

Anas platyrhynchos will hybridize with the native Black Duck (*Anas superciliosa*) and produce fertile offspring. Hybrids are often shot in Australia.

Established but uncommon species. A further seven species of birds are established in a small way in Australia. The Ostrich *Struthio camelus* is established in South Australia. The swan *Cygnus olor* is established on the Avon River, Northam in Western Australia. The Peacock *Pavo cristatus* is widely kept in captivity and is often free-ranging. Some are established on Rottnest Island, Western Australia. *Gallus gallus* (feral chicken) is often released, but the only known success is on Heron Island, Queensland. The Ring-necked Pheasant *Phasianus colchicus* has been widely introduced. It is established on Rottnest Island, Western Australia, in Tasmania and possibly some areas in southeastern Australia. The California Quail *Lophortyx californicus* is established on King Island. *Meleagris gallopavo* (feral turkey) is established on Prince Seal Island, Tasmania.

Several other species appear to have become extinct after a successful start. These include the Red-vented Bulbul *Pyconotus cafer*, the White-winged Wydah *Euplectes albonotatus* and the Red Bishop *Euplectes orix*.

At least 13 to 14 native species of birds have been transferred, introduced or reintroduced in Australia (see Table 10.3).

Reptiles. The only documented introductions of reptiles onto the Australian mainland are a gecko *Hemidactylus frenatus*, found in various settlements around the north coast from about Darwin to Cairns, and a blind snake, *Ramphotyphlops braminus*, around the Darwin area. There have been several introductions on Australian island territories, including *Hemidactylus frenatus* (Cocos (Keeling) Islands), another gecko *Gehyra mutilata* (Christmas Island), *Ramphotyphlops braminus* (Christmas Island) and a skink *Lygosoma bowringii* (Christmas Island) (Cogger, 1986; Cogger *et al.*, 1983).

Amphibians. The Cane Toad, *Bufo marinus*, was introduced into Queensland to control insect pests, particularly the cane beetle *Dermolepida albohirtum* (Frith, 1973). Many toads

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Table 10.3 Successful reintroductions and relocations of native vertebrates in Australia.

SPECIES	DATE(S) INTRODUCED	PLACE INTRODUCED
(a) MAMMALS		
<i>Ornithorhynchus anatinus</i>	1940	Kangaroo Island
<i>Phascolarctos cinereus</i>	1923→	numerous areas
<i>Bettongia penicillata</i>	1970's	SW Australia
<i>Lagostrophus fasciatus</i>	1974-1978	Dirk Hartog Island, W.A.
<i>Petrogale lateralis</i>	1973	West Island, S.A.
<i>Pseudochirus peregrinus</i>	1926	Kangaroo Island
(b) BIRDS		
<i>Cereopsis novaehollandiae</i>	1968	Tidbinbillia, Maria Island, Three Hummock Island and Kangaroo Island
<i>Alectura lathami</i>	1936	Kangaroo Island
<i>Geopelia placida</i>	1937-1940	Kangaroo Island
<i>Callocephalon fimbriatum</i>	1947, 1957	Kangaroo Island
<i>Cacatua roseicapilla</i>	various times	various
<i>Trichoglossus haematodus</i>	1960's	Perth, W.A.
<i>Cacatua galerita</i>	1930's	Perth, W.A.
<i>Dacelo novaeguineae</i>	1897-1912	Western Australia
	1905	Tasmania
	1926	Kangaroo Island
	1940	Flinders Island
<i>Menura novaehollandiae</i>	1934	Tasmania
<i>Dromaius novaehollandiae</i>	1957	Kangaroo Island
	1968	Maria Island
	1970's	locally in Queensland and New South Wales
<i>Neochmia ruficauda</i>	1980	Sydney, N.S.W.
<i>Lonchura castaneothorax</i>	1970's	Perth, W.A.
<i>Emblema temporalis</i>	1960's	Perth, W.A.
<i>Atrichornis clamosus</i>	1980's	Albany, W.A.
(c) AMPHIBIANS		
<i>Litoria raniformis</i>	1979 (?)	locally in South Australia
<i>Limnodynastes tasmaniensis</i>	1970's	Kununurra, W.A.
(d) REPTILES		
<i>Trachydosaurus rugosus</i>	1926	Kangaroo Island
<i>Tiliqua scincoides</i>	after 1926	Kangaroo Island

were released in the 1930's throughout the cane growing areas (Tyler, 1975). The species is now established from Cairns to Coffs Harbour.

Bufo marinus had no effect in controlling insect pests and was found to eat several species of useful insects including dung beetles (Tyler, 1975) and also indigenous lizards, snakes and a small marsupial (Covacevich & Archer 1975). It poses a severe threat to indigenous predators because of its poisonous skin secretions (Covacevich & Archer, 1975). The species does find some use as a teaching aid and as a test animal in medical research.

At least two species of amphibians have been established outside their native ranges in Australia (see Table 10.3).

Fish. Fifteen or sixteen exotic species of fish are established in Australia. The European Carp, *Cyprinus carpio*, is now widespread in eastern Australia. Perch *Perca fluviatilis* and the trout species *Salmo gairdneri* and *S. trutta*, are widely established in most states as game and sport fish. *Carassius carassius* and the Goldfish *C. auratus* are widely established. The Tench *Tinca tinca* and Roach *Rutilus rutilus* are also established, as are probably a few other species locally (Merrick & Schmida, 1984). The Mosquito Fish *Gambusia affinis* is now widely distributed from releases primarily directed at mosquito control (Coy, 1979).

The rapid spread of *Cyprinus carpio* since 1961 is the result of the introduction of a particular strain better adapted to Australian conditions (Ovington, 1978). The highly adaptable and competitive *Gambusia affinis* is replacing small native species of fish and reducing the survival of young sport and food fish (Ovington, 1978; Coy, 1979).

Several freshwater aquarium species of fish are established in tropical waters near Brisbane, Queensland. The Swordtail *Xiphophorus helleri*, Platly *X. maculatus*, Guppy *Poecilia reticulata*, Molly *P. latipinna* and Barb *Puntius conchonius* are established. *Tilapia mossambica* also may be established.

Introductions Of Invertebrates

Insecta, Colembola, Arachnida. There are probably more than 500 exotic species of the Insecta, Colembola and Arachnida established in Australia. The greater number of these arrived with man, were imported with their host animals and plants or were imported in goods and produce. A large group of selected exotic species are deliberate releases for biological control of pest plants and insects.

The magnitude of this invertebrate influx has made it necessary to omit reference to many species in this account.

Introduction of Insects for Biological Control. There have been numerous attempts by both Commonwealth and State authorities to control insects and plants by biological control in Australia. Fifty-one species of insects were imported between 1921 and 1935 and thirteen of these became established (Scott, 1981). In the early 1950's, CSIRO made 616 liberations of twelve beneficial parasites totalling more than half a million individuals against four pest species (Anon., 1954). There are now at least 83 species established (Carne et al., 1980) in Australia for biological control. Biological control programs have resulted in partial success against fifteen weed species before 1960 and partial success against five others since then (Waterhouse, 1979).

Introductions for Control of Pest Plants. The most famous and oft-quoted example of biological control in Australia is that of the introduction of *Cactoblastis cactorum* in the 1920's. The larvae of this moth in the space of five years brought about the collapse and destruction of 20 million hectares of the introduced Prickly-pear (*Opuntia inermis*) (Dodd, 1959; CSIRO, 1978). The plant, however, is not completely eradicated. Many other species were also introduced for control of Prickly-pear.

Before 1965, at least five insect species were successfully established to control the shrub *Lantana camara* in eastern Australia. The Central American bug *Teleonemia scrupulosa*, now common in Queensland and northern New South Wales, has exerted some control. From 1914 to 1973, 25 insect species were released for the control of *Lantana*, of which at least 10 became established (Willson, 1979).

Several insects were introduced to control such weeds as Water Hyacinth (*Eichhornia crassipes*) and Salvinia (*Salvinia molesta*). *Neochetina eichhorniae* and *Sameodes albipustulalis* are successfully attacking hyacinth (Room, 1979; Anon., 1979). The weevil *Cyrtobagous singularis* released in 1980 on the *Salvinia*-infested Lake Moondarra, Queensland, has achieved spectacular control in a short time (Ralph, 1982).

Other insects introduced for the control of pest plants include a weevil *Parapion antiquum*, to control Double-gee (*Emex* spp.) (Moulden, 1981; Scott, 1981). *Lixus cribicollis* has been introduced recently to control docks (*Rumex* spp.) and Double-gee (Richards, 1981). The beetle *Chrysolina quadrigemina* has materially reduced stands of the wort *Hypericum perforatum* (Sproul, 1981). The fly, *Procecidochares utilis*, was introduced to control the weed *Eupatorium adenophorum* (CSIRO, 1970). Several other insects have been introduced for the control of such weeds as Alligator Weed, Groundsel, Harissa Cactus, Ragwort and Skeleton Weed (Room, 1979; Willson, 1979; Cullen, 1979).

Introductions for Control of Pest Insects. The Vegetable Bug, *Nezara viridula*, is an introduced pest of crops such as beans, tomatoes and lucerne. It is widespread in Australia. An egg parasite, *Asolkus basalis*, released in the 1930's, has considerably reduced its population, but it continues to be a pest in some areas.

The Lucerne Flea, *Sminthurus viridis*, was noted in Australia in 1884. It subsequently has spread throughout (Wallace & Mahon, 1971b) the agricultural lands of the southern portion of the continent (Wallace, 1981). It is a pest of improved pastures and legume crops, particularly lucerne. *Bdellodes lapidaria*, a predatory mite which arrived with *S. viridis*, has failed to control its spread. The predator, *Neomolgus caphatus*, released in 1969, is having some effect on the numbers of *S. viridis*.

Halotydeus destructor from South Africa and *Penthaleus major* from Europe have spread rapidly since their arrival in Australia (Wallace & Mahon, 1971a). Both are widespread in southern Australia. *Penthaleus major* has spread further in-

land. The introduction of predatory mites *Anystis* sp. in 1965 shows promise of exercising considerable influence on *H. destructor* and *P. major* (Wallace, 1981).

Of the 118 aphid species present in Australia, most are immigrants (CSIRO, 1970). At least 46 species have been introduced from Europe on their host plants to which they are specific. A further four species arrived from America and another five are cosmopolitan species which have appeared here in the last 30 years. Many of them are of economic importance because of their effect on the vigour of their host plants. Maelzer (1979), however, states that there are 135 aphid species in Australia, 92 of which are introduced.

Several species of tiny parasitic wasps have been introduced for the control of aphids. *Aphelinus mali* has been successful in the control of the introduced *Eriosoma lanigerum* in Western Australia (Sproul, 1981). *Trioxys complanatus* was released to combat the aphids *Therioaphis trifoli* and *Acythosiphon kondoi*, both recent arrivals in Australia (Swincer, 1979; Sandow, 1981; Lehane, 1982). Other wasps released and established include *Praon exsoletum*, *Acythosiphon asychis* and *Aphidius ervi* (Swincer, 1979; Lehane, 1982).

Two small introduced predators, *Typhlodromus occidentalis* and *T. pyri*, have been successful against the mites *Tetranychus urticae* and *Panonychus ulmi* (Readshaw, 1979).

Of 22 potential control species introduced to contain the Wood Wasp *Sirex noctilio*, only three have been successful. These are the ichneumoid *Rhyssa persuasoria*, the cynipoid *Ibalia leucospoides* and the nematode *Deladenus siricidicola* (Taylor, 1981).

There are numerous introduced scale insects present in Australia. Some are pests of economic importance. Attempts have been made to control *Aonidiella aurantii* by the release of the parasites *Compierella bifasciata*, *Aphytis chrysomphali* and *A. melinus* (Maelzer, 1979). Control of *Saissetia oleae* was obtained in Western Australia with the introduction of the parasite *Scutellista cyanea* (Jenkins, 1946). *Anicetus communis* has assisted in the control of the scale *Gascardia destructor* (Anon., 1969).

In 1968, the first of a series of introductions of dung beetles was made in coastal north Queensland for the control of the Buffalo Fly *Haematobia exigua* and other fly species. *Haematobia exigua* arrived in Australia from Timor in 1820 on introduced water buffaloes *Bubalus bubalis*. It is now widespread and common across the north of Australia.

From 1968 to 1978, some 56 species of dung beetles were introduced (CSIRO, 1978). By 1978, eleven of these were established and a further 36 had been released. *Onthophagus gazella*, released in 1968, and *Euoniticellus intermedius*, released in 1971, are now spread over large areas of tropical and subtropical Australia (Anon., 1978). Others such as *Sisyphus spinipes*, *Onitis alexis* and *O. binodis* are now well established and spreading.

Accidental Introductions

Agricultural and Horticultural Pests. Besides those previously mentioned, a large number of insects has arrived accidentally in Australia.

The thrip, *Limothrips cerealium*, is an immigrant pest of cereals. The beetle, *Heteronychus arator*, is a serious introduced pest of maize in coastal New South Wales. Other introduced pest weevil species include *Bruchus pisorum*, a pest of cultivated peas, *Cylas formicarius*, a pest of sweet potatoes and *Graphognathus leucoloma*, which feeds on the roots of citrus trees. *Otiorrhynchus sulcatus*, *O. cribricollis* and *O. iscabrosus* attack fruit trees and strawberries. *Spodop-*

10. EXPLOITATION AND INTRODUCTIONS

tera litura, *S. mauritia* and *S. exempta* are widespread Old World pests. *Spodoptera litura* attacks cotton in the northwest and the other two species attack pastures in the north and east. The Codling Moth *Cydia pomonella*, attacks apples and pears and the Cabbage White Butterfly, *Pieris rapae* is also widespread.

The wasp *Sirex noctilio*, damages pines (*Pinus radiata*) and related conifers in southeastern Australia and Tasmania. The introduced "slug", *Caliroa cerasi*, is a pest of some fruit trees. The sawfly, *Schizocerella pilicornis*, mines the leaves of the introduced *Portulaca oleracea*. The wasp, *Aylax hypochoeridis*, causes galls in the flower stems of the introduced Dandelion (*Hypochoeris radicata*). Neither species is of economic significance.

Stored Grain and Stored Product Pests. Many of the introduced beetles and weevils (Coleoptera) are pests of stored products. *Stegobium paniceum* is a pest of drugs, stored food and other products. *Niptus hololeucus*, *Gibbium psylloides* and *Mezium affiniae* are household pests from the Mediterranean region.

Rhizopertha dominicana, *Tenebroides mauretanicus*, *Oryzaephilus surinamensis*, *Tribolium castaneum*, *T. confusum*, *Sitophilus granarius* and *S. oryzae* are grain pests of considerable economic importance. The cosmopolitan *Cryptamorpha desjardinsi*, *Nausibius clavicornis*, *Ahasverus advena* and *Cathartus quadricollis* are pests of dry stored food-stuffs. The cosmopolitan *Necrobia rufipes* infests ham, cheese, copra and carcasses.

Other pests of cereal products which have a world-wide distribution include *Gnathocerus cornutus*, *Latheticus oryzae*, *Palorus ratzeburgii*, *Alphitobius diaperinus*, *Araccerus fasciculatus* and *Anthicus floralis*.

A large group of introduced lepidopteran insects also attacks stored products. The cosmopolitan *Nemapogon granella*, *Niditinea fuscipunctella* and other stored product pests *Hoffmannophila pseudospretella*, *Endrosis sarcitrella*, *Corcyra cephalonica*, *Pyralis farinalis* and *Aglossa caprealis* are well established. The most damaging introductions are probably *Sitotroga cerealella*, *Ephestia kuehniella*, *E. elutella*, *E. cautella*, *E. figulilella* and *Plodia interpunctella*.

Besides these species at least five species of silverfish (Lepismatidae) have been introduced. They are often household pests. Nine cosmopolitan species of cockroach have been introduced. Several of the genera *Periplaneta* and *Blatella* are widespread pests. They destroy foodstuffs by eating them, but more importantly foul them with their excreta. A number harbour organisms pathogenic to man.

Pests of Man and Domestic Animals.

The lice, *Pediculus humanus* and *Pthirus pubis*, the fly *Musca domestica*, mosquito *Culex fatigans*, bed bug *Cimex lectularius* and the flea *Pulex irritans* travelled as "commensals" of man and arrived in Australia with the First Fleet.

Many species of lice infest domestic animals. Five introduced species of the genus *Linognathus* parasitize canids and ruminants in Australia. Four introduced species of the genus *Haematopinus* are important pests of domestic stock (CSIRO, 1970).

A range of fleas affects both man and his domestic stock. *Pulex irritans* occurs on man, *Ctenocephalides* spp. on dogs and cats and *Echidnophaga gallinacea* on poultry. Other species are found on introduced rats and the mouse.

The introduced fly *Stomoxys calcitrans* is cosmopolitan and common in Australia. It is an obligate feeder on livestock and man. *Haematobia exigua* is a major pest of cattle and

horses in northern Australia. The botflies *Gasterophilus intestinalis*, *G. nasalis* and *G. haemorrhoidalis* are introduced pests of stock.

Eighty percent of primary blowfly strikes in Australia are caused by the introduced *Lucilia cuprina*. This pest causes direct or indirect losses of millions of dollars annually to the sheep industry. *Lucilia sericata*, which was also introduced, is a pest in other countries, but is not important in Australia.

Two species of tick (Acarina : Ixodidae) have been introduced in northern Australia (Roberts, 1965; 1970). *Boophilus microplus* is now widespread; *Rhipicephalus sanguineus* is restricted in range. Both are implicated as vectors of serious diseases, some of which affect humans (Roberts, 1970). A third species *Argas* sp. (persecutes group) is widespread and affects mainly domestic poultry.

Other Pest Species. *Anobium punctatum* is a cosmopolitan pest of wood furniture. *Dinoderus minutus* infests bamboo and damages basketware and furniture. *Nacerdes melanura* is a cosmopolitan pest and breeds in wharves and old ships' timbers.

At least six species of introduced ants are present in Australia. *Iridomyrmex humilis*, *Technomyrmex albipes* and *Monomorium pharaonis* are pests in southern areas. *Solenopsis germinata*, *Tapinoma melanocephalum* and *Pheidole megacephala* are familiar nuisances in tropical Australia (CSIRO, 1970).

Seven species of spiders (Arachnida : Araneae) are established. Most have been introduced with Europeans and spread with settlement (Main, 1976). *Pholcus phalangioides*, *Achaearanea tepidariorum*, *Oecobius annulipes* and *Dysdera crocata* are cosmopolitan. *Scytodes thoracica* is widespread, but *Tegenaria domestica* and *Loxosceles rufescens* are restricted to some major cities. All are closely associated with human habitation.

Other Invertebrate Groups. At least six species of millipedes are established, some of which can cause economic damage (Baker, 1985). They include *Ommatoiulus moreletii*, *Brachyiulus pusillus*, *B. lusitanicus*, *Ophyiulus verruculiger*, *Brachydesmus superus* and *Oxidus gracilis*.

Nine to 10 species of exotic snails (Mollusca : Gastropoda) are established, including *Cochlicella acuta*, *Helix aspersa* and *Theba pisana*. Two introduced lymnaeid snails, *Lymnaea columella* and *L. tomentosa*, occur in eastern Australia. *Lymnaea columella* acts as an intermediate host of the Liver Fluke *Fasciola hepatica*. Five genera of introduced slugs are present, common species including *Milax gagates*, *Limax maximus* and *Arion intermedius*. Lumbricid and peretimoid earthworms also have been introduced and are now widespread. The glossoscolecid *Pontoscolex corethrurus* is widely distributed on the tropical and warm temperate east coast.

Apart from free-living forms, such as *Bipalium kewense*, several parasitic platyhelminths have also been introduced into Australia, but have not been included in this review. Many are of economic importance because of their effect on domestic grazing animals.

EXPLOITATION OF INTRODUCED ANIMALS

Before the release of myxomatosis and the widespread use of 1080 poison for the control of *Oryctolagus cuniculus*, an important industry was based on this animal. Commercialization reached a peak in the 1940's when 4.5 to 5.9 million kg of skins and up to 32 thousand tonnes of meat were exported. The export trade in meat and skins fluctuated erratically, depending largely on the overseas demand for the

products. The industry declined with increased rabbit control and the changes in fashion. A small export trade continues. Deer farms have been established in recent years, particularly in Victoria and Queensland, and an export trade supplies venison to Europe as well as Australian restaurants. A small export trade has developed for antlers and their velvet for use in Oriental medicine. Fox furs are exported in small quantities.

There has been a number of attempts to commercialize *Bubalus bubalis* since 1886. Until 1965, about 380,000 hides were exported (Tulloch, 1969; Ford & Tulloch, 1982). The record season for hides was in 1937-38 when 16,549 were exported (McKnight, 1976). The industry collapsed in the early 1950's because of competition from Asian markets and inept methods of curing (Ford & Tulloch, 1982). It has been re-established, however, and large numbers of buffalo now are slaughtered each year by two abattoirs which in 1981 returned \$7 million (Tulloch, 1983).

Several other feral animals also are exploited. There is a small export trade in live *Camelus dromedarius* to the Middle East (Anon, 1977; Newman, 1983). In the last twenty years, many *Capra hircus* have been shipped live from Australia, especially from Queensland, South Australia and Western Australia. Many also have been utilized by the pet-meat industry in Queensland and Western Australia. Recent studies suggest that some of these animals may be of use for a "cashmere" industry. Feral horses occasionally are caught and broken for use on pastoral leases or by private persons.

A few attempts have been made to exploit introduced species of birds. Attempts are being made to farm pheasants *Phasianus colchicus* and quail *Coturnix coturnix*, as table birds. The market at present appears to be small. Ostriches *Struthio camelus* were imported and farmed for feathers in South Australia in the early part of this century. The industry collapsed in the 1920's due to changes in fashion and the birds were released or abandoned to become established locally (Blakers *et al.*, 1984).

Possibly four species of insects have been exploited to some extent. *Tenebrio molitor* and *T. obscurus* are occasionally bred privately or in scientific institutions as food for reptiles and insectivorous birds. They are sometimes sold by pet shops for the same reason. Silkworms, *Bombyx mori*, may have been useful to early settlers. The Honey Bee *Apis mellifera* was deliberately introduced and is of considerable importance as a honey producer.

EFFECTS OF EUROPEAN MAN ON THE MARINE FAUNA

Explorers and merchantmen of Dutch, Portuguese and British origin may have sampled the Australian marine fauna on the western coast prior to settlement, as Captain Cook's men did in Botany Bay. The first sustained non-Aboriginal exploitation of the Australian marine fauna was not by Europeans, but by Indonesians fishing along the northwestern and northern coasts. European fishing followed closely the establishment of the settlement at Sydney Cove. As new coastal townships were founded, the area being fished increased, but not as rapidly as the exploitation of whales and seals which quickly spread to wherever concentrations of these animals could be found.

The first major fisheries in Australia were those to supply overseas markets and were sustained not by fish but by whales and seals. Exploitation of scaled fish grew slowly in competition with the supplies of red meat which became plentiful after the first few years of scarcity as the flocks and herds became established. Also, the apparent lack of schools

of fish as large as those with which the new settlers were familiar in the North and Irish Seas dampened enthusiasm for fishing in the rough seas of New South Wales.

Some attempts to remedy the deficiency were made by importing some European species, but the results were disappointing. As well as these deliberate importations, a certain number of non-commercial species have been introduced accidentally.

Exploitation of the Marine Fauna

Although the very earliest fishing efforts of the infant colony on the shores of Port Jackson were directed at survival the subsequent fishing activity has been aimed at satisfying commercial requirements and the recreational needs of a burgeoning population. During the 19th and early 20th Centuries, the collecting hobbies led to the removal of an unknown quantity of sea shells, corals and other forms.

There is scarcely a species of fish taken commercially which has not at one time or another been alleged to be overfished. For the vast majority there is no clear evidence that the condition complained of was not a temporary natural fluctuation in abundance. Consequently, many species which are important commercially will not be mentioned in this account, simply because, whatever suspicions there may be, there is no conclusive evidence of overfishing or depletion. Most, if not all, species which are fished to any considerable extent have a size distribution which is different from that of the unexploited stocks. This is an inevitable effect of fishing which does not in itself result in fewer numbers, but in a smaller average size of the individuals making up the catch.

The Fisheries

If one accepts the term "fishery" to cover the exploitation of all marine fauna the fisheries of Australian waters have been diverse. They include not only fishes, but also whales, seals, dugong, turtles, crocodiles, oysters and other molluscs and a variety of Crustacea and corals. The Australian fisheries were worth about \$440,000,000 to the primary producers in 1982-83. The weight of catch was about 170,000 tonnes (Anon, 1984), about eight times the catch of ten years before. This, however, represents only a fraction of the catch taken by countries such as Japan, which fishes more than seven million tonnes per year.

Whales: Herman Melville of literary fame is generally credited with taking the first whales off the Australian coast. Actually, there were several whaling ships already at anchor in Port Jackson when Melville's ship *Britannia* arrived to discharge her cargo of prisoners. The crew had spotted a large concentration of sperm whales south of Sydney and, with the cooperation of Captain Phillip, the cargo was discharged in record time to enable *Britannia* to go back to sea accompanied by another British whaler, the *Will and Ann* (Dakin, 1934).

Although the first whales taken by Melville and others were sperm whales *Physeter catodon*, the bay whalers, who operated from the shore both in New South Wales and Tasmania, generally took the Southern Right Whale *Eubalaena australis* which they knew as the Black Whale. As early as 1840, the pressure on the stocks was obviously leading to depletion and by 1845 the Right Whale no longer visited the Derwent Estuary nor most of the bays along the coast. By 1848, the sperm whales also were noticeably in smaller numbers. Some desultory whaling continued until 1896, but the American whalers who had dominated in the early days no longer brought business to Sydney and Hobart.

10. EXPLOITATION AND INTRODUCTIONS

Whaling had gradually spread along the whole southern coast of the continent and eventually up the western coast. But there, too, the fishery was virtually moribund after the 1860's. Minor attempts were made to revive the industry between the years 1918 and 1939. After World War II the Australian government opened a whaling station at Carnarvon in Western Australia and several private companies opened operations on both the eastern and western coasts. This whaling was primarily based on the Humpback Whale *Megaptera novaeangliae* which had been taken only when other whales were scarce in the early days of the industry.

The same stocks of humpback whales were hunted by whale chasers based on large factory ships which came from several countries, principally from Norway, Japan and Britain. Fin whales were the principal target of these whalers, but humpbacks were also taken. By 1954, the combined assault on the humpbacks had resulted in numbers and in an obvious decline in the mean size of the catch. By 1958, the two companies operating in Western Australia could not fill the quota allotted by the International Whaling Commission. In the eastern states, the first failure to fill a quota occurred in 1961.

Complete protection of the whales was agreed upon by most of the exploiting nations. After some twenty years of a high though not total degree of protection, humpback whales are once more appearing in increasing numbers along Australian coasts (Bryden, 1982; Palena & Palena, 1984).

Seals: When whales were scarce, the crews often turned to sealing and some of the less adventurous preferred the coastal work to the hazards of whaling in the open and often tempestuous seas. Four species of seals were hunted and, like the whales, overexploited. The Southern Elephant Seal, *Mirounga leonina*, is the largest of all seals. It is circum-polar, but all its larger colonies were ruthlessly exploited in the early 19th Century. King Island in Bass Strait was no exception. This was a breeding ground when sealing started. Although some flesh may have been eaten, the main purpose of hunting *M. leonina* was to render their blubber down for oil. From the small volume of oil per animal that was reported, all size groups apparently were taken (Ling, 1978). Before many years passed, the Elephant Seal disappeared from Bass Strait. In recent years, occasional specimens have turned up along the southern coasts of Australia. Breeding has not resumed at King Island although there have been recent records of isolated breeding on both the eastern and western coasts of Tasmania. There are breeding colonies on both Heard and Macquarie Islands and at Kerguelen and South Georgia.

Three species of eared seal also occur in Australian waters. The Australian Fur Seal, *Arctocephalus pusillus doriferus*, now inhabits the coasts from southern New South Wales to Tasmania and western Bass Strait. It is believed to be the species which the sealers all but eliminated in the 19th Century. Estimates of the present population vary between 20,000 (King, 1983) and 35,000 (Ling, 1979). Individuals even reach the southern coast of Queensland, but they usually stay close to rocky areas in the south. The size of the original population is unknown; consequently, so is the degree of recovery.

The New Zealand Fur Seal, *Arctocephalus forsteri*, is more wide-ranging than its Australian congener. It has breeding colonies as far west as the Recherche Archipelago as well as at Eclipse Island, at Southern Neptune at the entrance to Spencer Gulf and on Four Hummocks Island and Kangaroo Island. Undoubtedly this species also was taken by the sealers and badly depleted. Estimates of the numbers currently in Australian waters vary between 2,000 (King, 1983) and 5,000 (Ling, 1979).

The third species of eared seal is the Australian Sea Lion, *Neophoca cinerea*. Its present distribution overlaps that of the New Zealand Fur Seal, but extends up the western coast of the continent to the Houtman Abrolhos Islands. Dutch sailors are known to have eaten seal meat procured there. The eastern end of their range is now Kangaroo Island, but skeletal remains from historical times indicate that the species formerly extended through Bass Strait. Estimates place the population at about 5,000.

Dugong: In contrast to seals, the Dugong, *Dugong dugon*, is a tropical herbivore. In Australia, this sea-cow ranges from Shark Bay to Moreton Bay. Its natural range is far wider, reaching Mozambique in the western Indian Ocean and the Solomons and New Caledonia in the western Pacific and the Ryukus. Dugongs are used by indigenous peoples and were once welcomed to the table of explorers and ships crews for their flesh, hides and dugong oil. The Dugong is highly dependent upon sea-grasses, so that the tendency for sea grasses to disappear from some parts of Moreton Bay and other ports is a matter of concern (Young & Kirkman, 1975) (see also Chapter 57, this Volume).

The exploitation of Dugong by a growing native population needs close scrutiny (Marsh *et al.*, 1981) as do the effects of operations aimed at other species, such as mesh-netting for sharks (Heinsohn, 1972; Heinsohn *et al.*, 1976). Marsh (1986) concedes, however, that these concern are based mainly on assumptions about the accuracy of aerial surveys and of limited data on reproductive capacity. There is, nevertheless, good evidence that the number of dugongs marketed in certain areas of Torres Strait has declined since 1979. There is cause for concern even if the statistics are not conclusive.

Turtles: There are six species of marine turtle in Australian waters. They have been hunted by indigenous peoples both in Australia and in the neighbouring islands and were formerly exploited by Europeans. Today, they are protected except for the right of the indigenous people to take them for food.

The Green Turtle, *Chelonia mydas*, is regularly found in northern Australia from Shark Bay to Moreton Bay and sometimes strays well to the south. Carnivorous when young, they become vegetarian later in life. The flesh was once used for turtle soup; the skin makes good leather and the shell was used to make ornaments. Of world-wide distribution in the tropics, the Green Turtle is now rare except in Australian waters, but may well be declining there if anecdotal evidence of former numbers nesting on places such as Bramble Cay are correct (Limpus & Parmenter, 1986).

The Hawksbill Turtle, *Eretmochelys imbricata*, is the major source of the tortoise shell of commerce. This trade has declined with the competition from plastics, but the hunting pressure in much of the world has been maintained to produce turtle soup. The species is now rare except in Australia. Even here there is cause for concern as the eggs are harvested by islanders on almost every island where *E. imbricata* nests. The endemic Flatback Turtle, *Chelonia depressa* is abundant in the Kimberley region, along the north coast to Torres Strait. Specimens occasionally turn up along the Great Barrier Reef and the north Queensland coast near Bundaberg. The eggs are eaten by Aborigines and Islanders, but the flesh is generally regarded as inferior to that of other turtles. Possibly because of this reputation, the species was not regarded as endangered until recently, when observations in the Torres Strait region indicated heavy predation of the eggs by Islanders and destruction of nests by feral pigs on mainland beaches (Limpus & Parmenter, 1986).

The Pacific Ridley, *Lepidochelys olivacea*, is cosmopolitan in tropical waters. It is believed to be common in northern Australian waters, though most records are from Torres

Strait and the Cobourg Peninsula in the Northern Territory. The species is a popular food item in Central America, but the extent of Aboriginal exploitation is unknown.

The Loggerhead Turtle, *Caretta caretta*, occurs in the tropics throughout the world, but has become rare except in Australian waters.

The Leathery Turtle or Luth, *Dermochelys coriacea*, is the largest of turtles and attains a carapace length of over two metres. It is found in all tropical and temperate seas. *Dermochelys coriacea* is regarded as the most endangered species of turtle as its eggs are regularly plundered from its major nesting sites, including the Solomon Islands and Malaysia. Only small nesting groups are found on Australian beaches, mostly along a stretch of the central Queensland coast (Limpus, 1974).

Crocodiles: The Salt-water or Estuarine Crocodile, *Crocodylus porosus*, is the largest living reptile, reaching some seven metres in length. Its range extends from India to the Philippines, New Guinea and Australia. It has become relatively scarce in the western part of its range due to hunting pressure. It appeared to be heading towards a similar status in northern Australia until it became strictly protected. Under protection, the numbers have increased and are now causing concern for human safety in certain areas. The former status of this crocodile as endangered is now doubtful, at least in Australia. A number of crocodile farms now breed the species, but the wild population is also increasing steadily. Crocodile eggs and crocodile flesh are standard food items for Aborigines, but it is doubtful if the take is sufficient to influence the level of crocodile population.

The Freshwater Crocodile, *Crocodylus johnstoni*, does not normally enter marine waters but is mentioned here because its range overlaps that of *C. porosus* and it was also considered endangered until the moratorium on hunting was called.

Pearl Shell: The pearl oysters of several species were exploited from 1861 onwards in Western Australia and from 1868 in the Torres Strait region. The two largest-growing species of pearl shell live in Australian waters: the Black-lip Pearl Shell (*Pinctada margaritifera*) and the Gold-lip Pearl Shell (*Pinctada maxima*). The main object of the fishery was for the shell which provided mother-of-pearl used in the manufacture of ornaments of many kinds. Pearls were but a lucrative side-line. Extensive fishing resulted in a decline of the abundance of the pearl oysters on the beds. In 1890, the average take of a pearling lugger in the Torres Strait fishery was seven tons, by 1898 it had dropped to about two tons and in 1905 to 1.5 tons.

In Western Australia the average take was greater: 12 tons in 1905 and rising to 15 tons in 1948 after the grounds were rested during the war years. In the 1950's the fishery declined, but perhaps not entirely due to depletion of stocks, as plastics had become competitive at this time and eventually almost entirely supplanted pearl-shell in both the button and ornament trades. The fishery would have disappeared altogether had it not been for a demand to supply live oysters to the culture pearl farms which were being developed in northern Australia. The production from the culture pearl industry in northwestern Australia alone is now worth over \$40 million per year.

The stocks of pearl oysters in the Torres Strait are reported to be severely depleted. This is attributed by Yamashita (1986) to the effects of the oil spill from the *Oceanic Grandeur* in 1969. Pearl oysters fished soon after the oil spill and the associated addition of detergents were in uniformly poor condition and mortality was high. Since that time there has been no significant spat-fall. As recently as 1980 the "Old Grounds" were reported to be a desert. But a survey in 1984

showed that sea-grasses and sponges have started to repopulate the area, though there was no evidence as yet of an increase in the number of pearl oysters. There are also suspicions that the stocks in northwestern Australia have been overfished. The take has declined markedly since 1981 (Dybdahl & Rose, 1986).

Trochus: Other shells besides pearl-shell have a rich nacre, but few have a shell thick enough to withstand cracking or punching for buttons. *Trochus niloticus* was one of the few. These prosobranchs live in comparatively shallow water on the reefs of northern Australia and on the Great Barrier Reef. By 1939, the *Trochus* beds were reported to be depleted, but the enforced rest over the war years enabled a dense population to become established. A revitalised industry was expanding when the competition from plastics brought an untimely end to the business.

There has been a recent revival, however, because certain of the fashion houses in Europe have decreed that the buttons on their shirts and blouses should be "natural" and not plastic. There is no current sign of depletion in the Great Barrier Reef region, but fears have been expressed for the future, because elsewhere in the Pacific *Trochus* have been overfished with a consequent increase of pressure on the Australian stocks (Nash, 1986).

Scallops: Apart from squid, octopus and cuttlefish, molluscs are either attached or are slow-moving and most vulnerable to capture. Scallops can move by a kind of jet propulsion, but very inefficiently. The history of the Tasmanian scallop fishery goes back at least to 1923. From its beginnings, the fishery experienced great fluctuations associated with the varying success of the spat-fall. Even the dominant species in the catch varied from time to time. In the 1920's, almost equal numbers of commercial scallops *Notovola meridionalis* and doughboys *Mimachlamys asperimus* were taken, with queens *Equichlamys bifrons* in smaller numbers. Then in the 1930's, *Mimachlamys* predominated until 1938, after which *Notovola* provided almost all the catch.

After 1948, the original beds in the D'Entrecasteaux Channel declined. Commercial scallops almost disappeared and *Mimachlamys* became dominant, but still in so few numbers that the beds were closed to dredging. Whether the decline was due to natural fluctuations or to the introduction of ever more efficient scallop dredges is still debated. The failure of the channel beds led to successful searches along the east and north coasts of Tasmania. More importantly for the scallop-eating public, new beds were discovered in Port Phillip Bay where an industry started in 1963. By 1965 the latter beds were producing more scallops than Tasmania had managed in its heyday. The populations on the Port Phillip beds have fluctuated over the years, but have escaped the catastrophic crashes which were typical in Tasmania. Hopefully, the management regime imposed in Victoria will stabilize the populations (Dix, 1982).

Abalone: Four of the fifteen species of Australian abalone are sufficiently large abundant and palatable to be marketed. The most important commercially is the Black-lip Abalone, *Notohaliotis ruber*, which occurs in all southern States. Not so abundant, but preferred by processors because of its white flesh, is the Green-lip Abalone, *Schismotis laevigata*. It is easier to collect than *Notohaliotis* because it lives in more exposed places. The Round Abalone, *Notohaliotis conicopora*, is more common in South Australia than in the other States. The Red Abalone, *Marinauris roei*, is smaller than the other species and the demand for this species has fluctuated.

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All abalone species have fluctuated in abundance over the years and overfishing has certainly contributed to this situation. Current management regimes appear to have produced a reasonably stable fishery. The heavy fishing probably keeps the numbers lower than in the unfished populations, but there is no evidence that any species is endangered.

Oysters: The Port Lincoln or Mud Oyster *Ostrea angasi* once provided a flourishing industry in South Australia, Tasmania, Victoria and southern New South Wales. By the end of the 19th Century this prosperous fishery was depleted. Despite an almost complete freedom from any exploitation, save amateur reef picking, for more than 80 years and despite the presence of good clutch material, populations have remained low.

The Sydney Rock Oyster (*Crassostrea commercialis*) has survived an even longer period of exploitation. By the time the wild stocks were showing signs of depletion, an elaborate system of oyster culture had been devised in New South Wales. The oyster farms themselves provide a huge reservoir of broad stock. Reef oysters are gathered in parts of north-western Australia and in Queensland but are underfished at present, although amateur gathering has denuded rocks near populated areas.

The Shell Trade and Giant Clam: The sea shell trade, which caters to specimen shell collectors, was worth approximately \$2.5 million in 1986. Some 90% of the trade is in endemic species (Australian National Parks and Wildlife Service data). The major families exploited are volutes (Volutidae), cowries (Cypraeidae), cones (Conidae), murex (Muricidae), strombs (Strombidae), mitres (Mitridae) and olives (Olividae). Many endemic species are limited in their distribution and intensive collecting of desirable species has already led to depletion (Barnett, 1986). The poaching of the Giant Clam, *Tridacna crocea*, by foreign fishermen has been sufficiently obvious to raise severe fears for its survival. A program is under way at James Cook University to breed the clams artificially.

Rock Lobsters: Known more familiarly to older Australians as crayfish, two of the several species that exist in Australian waters form the basis of one of Australia's richest fisheries. The western Rock Lobster, *Panulirus cygnus*, has repeatedly been alleged to be overfished. This fishery is most closely monitored in Australia. Prompt management measures taken whenever signs of stress have appeared have kept the stock at a reasonably stable level. The catch fluctuates about 9,000 tonnes per year and earns over \$30 million in export earnings alone per annum.

Each female produces between 100,000 and 250,000 eggs which hatch into a larval form very unlike the parent. A later larval stage, the glassy, flattened phyllosoma, floats in the seas for several months before returning to settle in the coastal reefs. At the end of the larval life, *Panulirus* individuals metamorphose into adult-like forms. Once settled, they tend to stay in a restricted area. Such a life history could lead to marked differences in the settlement rate from year to year. Although there is evidence that fishing pressure periodically leads to a catch that is below optimum, there is no evidence that the species is endangered.

A different species is distributed along the coasts of South Australia, Victoria and Tasmania. The Southern Rock Lobster, *Jasus lalandei*, is a southern species of circumpolar distribution. It, too, has often been claimed to be overfished, but years of poor catches have generally been succeeded by better years without any apparent change in the fishing pressure. While there is evidence of an effect on recruitment and catch as a result of fishing intensity, there is no such evidence in the southern fishery (Kesteven, 1966).

Prawns: Prawns are an annual crop, the young of one year being the breeders of the following year. As survival of larvae fluctuates widely as a result of hydrological and other environmental conditions, the catch can vary widely from year to year. Claims that prawn stocks are overfished or depleted are regularly made, but none have been sustained over any considerable period. Natural fluctuations tend to mask any correlation with the effects of exploitation. Rainfall is known to affect the catches (Thomson, 1955; Ruello, 1973). Destruction of the juvenile habitat of prawns through drainage alterations (killing off sea-grass beds and mangrove stands) probably has a greater effect on prawn numbers than does fishing (Coles *et al.*, 1985).

Mullet: Prior to the development of the rock lobster, prawn and tuna fisheries, Sea Mullet *Mugil cephalus* contributed more to Australian fish catches than any other species. The species consequently received much research attention. It has often been claimed to be overfished. The probability is that this species is being fished to capacity but there is no evidence of a depletionary trend (Thomson, 1950; 1953). This is probably the case with most of the inshore and estuarine species that are favoured commercially, but none has had the extensive study that the mullet has received.

Tiger Flathead: From its start in 1915, the trawling industry of southeastern Australia was sustained in its early years by the popularity of the Tiger Flathead, *Neoplatycephalus richardsoni*. By the 1950's, the catches of flathead were declining. The theory that overfishing had reduced the stocks was supported by the increased abundance of the species following the respite from fishing during the war years (Fairbridge, 1952; Houston, 1955). Overfishing may not be the whole story. When the Federal Research Vessel *Endeavour* discovered the trawling grounds during its surveys between 1909 and 1914, giant sponges and other large marine growths were abundant in the hauls. As the commercial fishery developed, such material was regarded as trash which clogged or even tore the nets and prolonged the time it took to sort the catch on deck. Consequently, the trawlermen adopted the practice of either taking the trash ashore or let it die on deck before reconsigning it to the deep. Such large growths are lacking on the well-worked trawling grounds today. This must have altered the habitat as far as food and shelter are concerned, and correspondingly, the proportions of fish species supported by the grounds may well have changed. The Tiger Flathead has not disappeared and is probably not endangered, but it is undoubtedly less abundant now than it was in the early days of the trawling industry.

North-west Fishes: Another example of altered proportions of fish species following exploitation of a virgin stock is demonstrated by the history of fishery on the North West Shelf. When trawling first commenced in 1961, lethrinids (emperors) made up between 40% and 50% of the catch. By 1976, Lethrinidae formed only 7% of the catch. Lutjanidae (sea perches) also declined from 23% to 12% of the catch. Nemipteridae (threadfins) dropped only slightly from 11% to 10%. Synodontidae (lizardfish) increased from 10% to 11.5%. Balistidae (triggerfishes) increased from 7% to almost 9%. Mullidae (goatfishes) which had been a very minor component, increased to 13% of the catch. Significantly, those species which have declined are those which are associated with sponges and soft corals, which would be trawled with the fish. Those that increased in proportion are species which are associated with sandy bottoms (Young & Sainsbury, 1985).

Whitebait: Australian gourmets once relished an entrée of Whitebait *Lovettia sealii* from the rivers of Tasmania. These little fish are sea-going, but after an absence of about a year they return to the rivers to spawn and to die. Because they

habitually swim upstream against the banks of the streams they are vulnerable to the fine-mesh nets in which they are taken (Blackburn, 1950). The stock has been decimated. Whitebait are protected under Tasmanian law and while they have not regained their former abundance, there is evidence that the population is increasing (Anon, 1968).

Tuna: A number of species of tuna inhabits Australian seas, but only the Southern Bluefin Tuna, *Thynnus thunnus mccoyii*, is important to Australian fishermen, although Japanese long-liners also take other species not far from our coasts. The Southern Bluefin ranges widely from New Zealand across the Tasman Sea to the south coast of Australia, up the west coast to south of Java and across the southern Indian Ocean to southern Africa. Exploited inshore by Australian fishermen near Albany, Port Lincoln and Eden and taken by Japanese fishermen offshore, the species is showing every sign of overfishing (Murphy & Majkowski, 1981). International action is under way to rationalize the exploitation of this resource.

Sharks: Only two species of shark have formed the basis of a continuing fishery in Australian waters: the School Shark, *Galeorhinus galeus* and the Gummy Shark, *Mustelus antarcticus*. They provide a fishery in the Bass Strait region, extending to southern Tasmania, New South Wales and South Australia. The fishery was small until World War II, when the need for a substitute for cod-liver oil was solved by using the large livers of the School Shark. Vitamin D, which was the main useful product of the oil, was synthesized cheaply after the war, so the demand for shark liver oil disappeared. By this time, however, the flesh had found a firm place in the Victorian markets as "flake".

Opinions differ as to whether the School Shark is or was overfished. Certainly, such a slow-growing animal of low fecundity is liable to depletion. By the late 1950's, the average size of shark taken was dropping, a good indicator of incipient overfishing. A reprieve came unexpectedly, when it was discovered that the flesh had a mercury level well above that regarded as safe for human consumption. At first, industrial pollution was suspected, but it has since been demonstrated that many large-growing fishes, including sharks and the big-game fish, such as marlin, accumulate mercury throughout life. Smaller sharks have relatively little mercury content and may be marketed. Larger sharks which may not be taken provide an effective brood stock.

The diminution in the available stock of School Shark has increased the pressure on *Mustelus* and there are fears that there is serious overexploitation of this species. Melbourne's supplies of flake may well be endangered.

Barramundi: The Barramundi, *Lates calcarifer*, is a diadromous fish, i.e. it is capable of passing from fresh to salt water and vice versa. The young enter the tropical rivers during the wet season and spread with the flood waters over the floodplain to populate billabongs, lakes and ponds as well as the main river channels. In a subsequent wet season, the mature fish pass down the rivers to sea, where they spawn. At this stage they are particularly vulnerable, especially to unscrupulous people who set nets from bank to bank, despite regulations to the contrary. The drop in abundance has been so obvious in Queensland and in the Northern Territory that management measures such as bag limits and closed seasons have been introduced. One consequence of the lessened supply has been that some less-favoured tropical fish have been delivered to market as "Barramundi". The high market price and the tolerance to changing conditions make this species an obvious candidate for fish farming and experimentation is under way in several places.

Groper: When considering overfishing, most people think in terms of professional fishermen; but fishing pressure by amateur fishermen is also great and in some areas equals that of the professionals (Thomson, 1959b). One group of fishes that has become scarce primarily because of amateur fishing is the gropers and rock cods. The large size of these fishes has made them sought-after prizes by spear-fishermen. One of the largest Australian fish, the Queensland Groper *Epinephelus lanceolatus*, is now protected from spear-fishing because its numbers became seriously reduced after spear-fishing became popular. Populations of other large-sized species, such as the Black Rock Cod *Epinephelus daemelii* and the Barramundi Rock Cod *Cromileptes altivelis* were also severely affected before spear-fishing was discouraged.

Despite the similar popular name, the red and blue gropers of southern Australia belong are not related to the Queensland gropers. At one time, several species were recognized on the basis of colour pattern, but many of these are now regarded as merely colour variants and only two species are recognized. These are the Western Blue Groper *Achoerodus guild* and the Eastern Blue Groper *A. viridis*. Because of an evident decline in abundance there is a ban on spear-fishing in both Western and South Australia. A similar ban was imposed on the taking of *A. viridis* by spears and a bag limit placed on anglers. Subsequently, some commercial fishermen devised a bottom-set net for use near reefs which proved so effective in catching Groper that a total ban has been imposed on the sale of Groper in New South Wales (Anon, 1980).

Estuarine Perch: The Estuarine Perch *Macquaria colonorum* lives in coastal rivers from northern New South Wales to the mouth of the Murray River. It is most common in the tidal estuaries, but enters freshwater. An apparent decline in abundance resulted in legislation in New south Wales to prohibit commercial exploitation, though a sport fishery is allowed. This species is very similar to the Australian Bass (*Macquaria novemaculatus*) and some authorities regard them as conspecific, although some clear differences indicate at least racial or subspecific distinction.

Introduced Marine Fauna

Salmonids: Atlantic Salmon *Salmo salar*, Quinnat Salmon *Oncorhynchus tshawytscha*, Brown Trout *Salmo trutta*, Rainbow Trout *Salmo gairdneri* and Brook Char *Salvelinus fontinalis* have been introduced into Australia to provide sport in inland waters which are cool enough to support them. The species also have sea runs in their native lands and this could be expected in Australia. Neither sea-runs nor permanent populations of the two species of salmon have been established in Australia, but reintroductions are periodically made. Some Atlantic Salmon are believed to survive in Lake Jindabyne and Quinnat Salmon released in Lake Purumbete in 1976 may still survive.

The Brook Char is established in some of the tablelands of southern New South Wales and after some initial failures to establish seems to be persevering in Lake Clarence in Tasmania. This species is not even abundant in its native lands, which might explain its limited success in Australia where the Brown and Rainbow Trout have been well established (McDowall, 1980). Both the Brown Trout and the Rainbow Trout have become established in cool rivers, especially in the highlands of New South Wales, Victoria, South Australia and Tasmania, and in a few rivers in southwestern Australia. On the whole, the Brown Trout seems to have been more successful, but there are rivers where the Rainbow Trout is more abundant. Sea runs of trout have been established in Tasmania (Nicholls, 1957).

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Mosquito Fish: This little fish (*Gambusia affinis*) was introduced to control mosquito larvae. It is generally regarded as an inhabitant of fresh waters, but it penetrates the upper reaches of estuaries and is found in brackish lagoons around much of the Australian coastline. It is found around much of the coast-line of the country. *Gambusia* is believed to have eliminated some of the smaller native fishes, but it is a difficult matter to prove.

Gobies: Unlike the fish mentioned above, two species of Goby appear to have reached Sydney Harbour by accident. *Tridentiger trigonocephalus* and *Acanthogobius flavimanus* are natives of Japan and have also been reported to be introduced into California. They are believed to have reached New South Wales in water ballast which the ship concerned discharged into the harbour. Having become established, they presumably compete with native species for resources (Hoese, 1973).

Sea Bass: Another Japanese fish, which grows to at least a metre and is carnivorous, has been taken in Pittwater near the mouth of the Hawkesbury River. Only two specimens have been caught, 18 months apart and of the same age-group. This is the Sea Bass *Lateolabrus japonicus*. Presumably this, too, is an accidental introduction. Whether the species becomes established depends upon whether sufficient numbers exist to form a breeding stock (Parr, 1985).

Plaice and Sole: In 1902, H.C. Dannevig, who was later to become the first Commonwealth Director of Fisheries, was employed by the New South Wales government as a "Fisheries Expert" and charged with the responsibility of acclimatizing suitable schooling fish from the North Sea to the waters of New South Wales. Several hundred Plaice *Pleuronectes platessa* and a lesser number of Sole *Solea solea* were transported successfully by sea to Sydney. After acclimatization in pens constructed in Port Hacking, they were released, never to be seen again.

Pacific Oysters: Prior to World War II, the CSIRO Division of Fisheries and Oceanography had planned to introduce a species of oyster (*Crassostrea gigas*) into southern Australian waters to fill the commercial niche left by the depletion of stocks of the Port Lincoln Oyster. In 1947 and 1948, large numbers of these oysters were imported to Tasmania, Victoria and Western Australia. The oysters appear to have died out in Mallacoota and in Oyster Harbour, but those in Tasmania have flourished and now form the basis of an oyster culture industry (Thomson, 1952; 1959a).

The natural spread, as well as deliberate transport by Man has moved the oysters from one estuary to another. In some places, such as the Tamar River and the Derwent River, despite abundant oysters, industrial pollution makes them unfit to eat.

Benthos: Several sedentary organisms which are carried as fouling on ships' bottoms can be found in benthic associations along parts of the Australian coasts where they were formerly unrecorded. They belong to several groups:

Bryozoa: *Bugula flabellata*, *Conopeum tubigerum*, *Schizoporella unicornis*, *Watersipora cucullata* and *Anquinella palmata*;

Polychaeta: *Mercierella enigmatica*;

Cirripedia: *Balanus* sp.;

Mollusca: *Thecacera pennigera* (nudibranch), *Musculista senhousia* (bivalve).

None of these were recorded by the early naturalists who studied the fauna attached to rocks and other underwater and intertidal surfaces. Some, such as *Watersipora*, are so obvious that they could hardly have been overlooked. Their patchy distribution around the coast indicates that their probable mode of introduction was by ships (Allen, 1953).

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11. CULTURAL VALUES, CONSERVATION AND MANAGEMENT LEGISLATION

GEORGE R. WILSON

INTRODUCTION

The Australian fauna is now generally regarded as having great cultural value and belonging, in a general sense, to the world cultural heritage. This value, however, has not always been recognized, although Aboriginal Australians certainly placed great economic and spiritual significance on the fauna. When the pastoralists, agriculturalists and, subsequently, mining industrialists began pushing inwards from the coast at the beginning of the 19th Century, they regarded the fauna as one of the components of the bush which had to be mastered. The self-set task of the pastoralists, for example, was to replace the fauna with alien species more readily capable of producing saleable products. This perspective persists amongst some agricultural developers today, although the most aggressive exponents have softened their stance. In the last quarter century, fauna conservation and management practices and corresponding legislation have emerged that reflect a much more sympathetic public attitude.

Nevertheless, vast improvements are possible in current wildlife conservation legislation and management practice. Contemporary conservation issues are highly politicized and rarely based on biology. Detailed biological information such as that contained in these volumes of the *Fauna of Australia* is used insufficiently in the process of fauna policy development. Decisions are often influenced and determined by sensational and emotional presentations rather than scientific assessment. For example, a very newsworthy subject such as the export and subsequent fate of zoo-bred koalas attracts far more comment and recognition than the programs of those State and Commonwealth authorities engaged in the protection of the habitat and management of thousands of wild koalas upon whom depend subsequent generations and the survival of the species. Because the emotional aspects of our wildlife (which are important) are regarded as more newsworthy than factual understanding, scientists are rarely involved in the public debates about wildlife.

In this Chapter, these public attitudes are discussed together with the value of the fauna, including ecological, economic, cultural, aesthetic, scientific and recreational aspects. The way they influence and are reflected in current conservation management, attitudes to exploitation and legislation including host/vector problems, pest control, public health, veterinary and medical legislation, import and export are considered and suggestions for future conservation aims are proposed. The emphasis is on terrestrial vertebrates.

PUBLIC ATTITUDES

The larger fauna are associated closely with the Australian identity. The kangaroo, which appears on the national crest, is one of the strongest symbols of Australia and is utilized for this purpose in many ways such as the boxing kangaroo of the America's Cup yacht Australia II and the flying kangaroo of the national airline QANTAS. Fauna features prominently in Aboriginal art and is the motif on the reverse side of Australian coinage.

A growing proportion of the urban population regards wild animals as sacrosanct, not to be killed or interfered with in any way. The notion is that wildlife have rights and should be able to lead unimpeded lives. If widely adopted, this attitude would have profound ecological consequences. It could, for example, lead to an uncontrolled increase in certain species, such as rabbits, which would have undesirable consequences for the indigenous fauna.

Aesthetic appeal, public concern and legal protection are correlated. The Koala (*Phascolarctos cinereus*), for example, is a popular animal which generates emotional attitudes. As a result, there is an extraordinary degree of protection for the species under State and Federal legislation. This cultural importance does not come from a rational assessment of the status of the species. Strahan (1982) suggests that the widespread revulsion of the Australian urban population against the slaughter of koalas in the first quarter of this century may have been due more to an unconscious association of koalas with babies than on rational assessment of the effect of the shooting on populations. Although now fashionable to vilify the trade in koala skins and to claim that it brought about the species near extinction, there is no evidence to support this view. The industry was a response to an abnormally high density of koalas following the easing of pressure from predation by Aborigines and dingoes. That koalas are most common in Queensland, where the species was most recently exploited with greatest intensity, suggests that hunting did not have a serious impact on the species. Community attitudes based on aesthetic appeal are extending to a larger number of species, but may not be for the good of all taxa.

Protection is advocated by some on an aesthetic basis on what might be called a "cuddliness index". On such a scale, koalas score very highly and fruit bats, rodents, reptiles and invertebrates very low. Ironically, this is a form of speciesism, the attribution of superior status to one species over another. Speciesism is a term developed by animal liberationists (Singer, 1975) to describe the way humans dominate other animal species for their own ends.

An even higher proportion of the community agrees that animals should be spared suffering and cruelty. They do not go so far as to argue for total protection of all fauna in all circumstances and they generally accept that when species such as kangaroos occur on land used for primary production, there may be the necessity to kill them, providing it is done as humanely as possible. The issue, nevertheless, is emotive and the controversy is compounded further because assessment of the extent of alleged damage is usually subjective. Some graziers will tolerate more kangaroos than others and a population level which is excessive cannot be defined.

The scientific value of fauna also differs with the perceptions of the beholder. If one were to attempt to quantify values, the task would be most difficult, involving the philosophy of science and assessments of cultural and other values. The Numbat, (*Myrmecobius fasciatus*) for example, has scientific worth as the only living member of the Myrmecobiidae. Attractive, diurnal and of cultural and heritage value as the

Western Australian fauna emblem, it is also extremely endangered. The Marsupial Mole (*Notoryctes*) is also of major scientific importance as the only fossorial marsupial and sole member of the Notoryctidae. The Plains-wanderer (*Pedionomus torquatus*) is the only member of its family. Its range has shrunk greatly since settlement and it has disappeared from most areas where more intensive forms of agriculture are practised. The gastric-brooding frogs of the genus *Rheobatrachus* also have special scientific value as a potential source of medical information in the suppression of autodigestion. All these species would probably rate highly in any quantification of scientific value.

Contribution to Ecological Stability

Public attitudes are now changing to include the perspective that fauna is part of the land's character and vitality and an essential part of the ecology and economy of the Australian community. Fauna is a component of the many ecosystems which interact with domestic animals and plants and their environments in very complex relationships that support human life.

Although scientific understanding of such matters is imperfect, enough is known to generalize that diversity, or number of species in ecosystems, is proportional to ecosystem stability. Resilience of ecosystems will be greater if they are made up of a large variety of species and when they contain a diversity of habitats providing protection from disturbance. When species become unusually rare or extremely abundant, variations to ecological processes are indicated. Ecosystems are dynamic and alterations in the population size of component species can follow disturbance by agents such as fire, drought, disease, grazing and predation. Ecosystems composed of single species, often of uniform genotype, such as are found in agricultural production systems, are less resilient in the face of disturbance than natural communities with diverse assemblages of animals. To ensure maximum stability, a diversity of fauna species should be present. Unfortunately, however, they often constitute a threat to the agricultural production systems and reduce, or are perceived to reduce, economic returns.

Genetic variety is also important within a species, because in the longer term it provides the material for adaptation in response to future changes in environment and in the short term improves the ability of species to withstand the impact of diseases and pests. Both the diversity of species in a community and the number of individuals in the population of a species are critical to the survival potential of species.

Faunal species have particular value as indicators of environmental change. By observing the fauna, we can assess the status of the ecosystems in which humans live. Fauna and flora can provide advanced warning of environmental deterioration that may directly affect human lifestyles or result in a decline in longevity. Biological indicators in the monitoring of heavy metal build-up and pesticide residues is an example. This is another fauna contribution to human cultural survival.

Paradoxically, many Australians believe that Australia is still waiting to be colonized and developed. This has greatest impact on fauna where agricultural developers continue to replace native species with exotics. They think the country is so vast that it has an unlimited capacity to supply resources and that there are no limits to the ability of life support systems to withstand human impacts. This is a fallacy; there can be no doubt that values must change to recognize the importance of ecological stability. Current stresses upon the ecosystems which support the Australian fauna are not widely recognized. The high standard of living enjoyed by most

Australians increases the demand on resources and causes greater likelihood of disturbance, especially because the demand is exponential and linked to growth in population.

Continuous growth in population and *per capita* demand for resources is inconsistent with the maintenance of essential ecological processes and life support systems, including the survival of the fauna. As more people transform raw materials into commodities, rates of depletion increase and as more commodities are transformed into waste, pollution increases. Australia's population is expected to be around 20 million by the turn of the century, which can only result in increased pressure on the fauna through demands on the resources, particularly in the east and southwest, for food, housing, transport, energy and recreational facilities. The need for food for a growing world population adds to the demand on export-oriented Australian primary industries.

Economic Production

Fauna can have value either as an asset or a liability. In economic terms, an asset is either a saleable product or, less directly, has cultural or heritage value.

The asset values are additive for species which are attractive to tourists. They have economic, cultural and heritage value. Economists attempt to measure these values through a variety of complex techniques. One assesses the opportunity cost by determining the amount of benefits a person is willing to forego to enjoy another set of benefits. For example, the amount a bird-watcher says he would have to be paid to give up a day's outing is the expressed opportunity cost. Another costing is based on the value of timber or agricultural production that the primary producer finds acceptable to forego to protect the habitat or to tolerate the damage done by fauna. This amount is the minimum value attributable to fauna (and other wildlife) in that situation.

Faunal species that are pests are liabilities and have a negative value where they come in conflict with either agricultural production, human habitation or other aspects of human activity. Often, the activities of man have increased fauna numbers to pest proportions. In the mid-19th Century in eastern Australia there was an enormous increase in numbers of certain faunal species following major changes in land management, the dispossession of the Aborigines, the partial removal of dingoes and the laying of poisonous baits which killed off large numbers of carnivorous birds. In both New South Wales and Queensland, Acts were passed making it compulsory for the squatters to destroy kangaroos and other pests. Levies, which were rated by the number of sheep and cattle that a landholder carried, were raised to pay for bounties on species such as "wallabies, kangaroo rats, pademelons, wombats, native dogs, eagle hawks, and crows in addition to hares and foxes". There were also reports of vast increases in the numbers of possums, emus, cassowaries and flying foxes (Frogatt, 1913).

Faunal species that are direct economic assets are often hunted to produce saleable products such as meat, fur or hides for human need. Such uses and values were, of pragmatic necessity, high in the very first days of settlement, although today the full economic value of the fauna is rarely realized. The predominant Anglo-Celtic culture of white Australia makes relatively little use of game meat and game products from terrestrial fauna. Nevertheless, hunting of fauna (and, of course, fishing) does continue. Hunting can be considered under three categories: sport, pest control and commerce.

Sport hunting is often closely associated with pest control, especially where agriculturalists encourage amateur sport hunters to assist control of unwanted macropods on their

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properties. Small macropodids such as Red-necked and Agile Wallabies are taken for sport, for pest control or for commerce (such as crayfish bait and for dog food on properties that have working dogs). The larger macropodids are also hunted for many of these reasons, especially where a commercial industry is not permitted, such as in Victoria and the more intensively settled areas of New South Wales. Apart from Tasmania, where the sporting and recreational aspects are traditional and are incorporated in law, much of this hunting is strictly illegal.

The cultural, aesthetic and legal restraints that apply to restrict the commercial value of the fauna are widespread and complicated. For example, commercial sale of the products of the larger macropodids is legalized throughout Australia, but the value of the animals in the wild is constrained. The hunting of kangaroos for commercial purposes is permitted only under licence and in certain areas. It is not allowed at all in Victoria, Northern Territory and the Australian Capital Territory. At the national level, the Commonwealth Government permits kangaroo meat and skins to be exported, but only in the name of controlling populations and mitigating the damage done to agricultural production. The industry does not have the objective of being a resource harvesting or wealth-creating enterprise. Nevertheless, it was valued at about \$10 million per year in the early 1980's and quotas are set for the taking of approximately two million animals each year. Uses include pet food, the skin trade and meat for human consumption, both domestic and overseas.

The species of marsupials which are hunted for commercial purposes are the most abundant. They are:

Red Kangaroo, *Macropus rufus*;
Eastern Grey Kangaroo, *Macropus giganteus*;
Western Grey Kangaroo, *Macropus fuliginosus*;
Euro or Wallaroo, *Macropus robustus*;
Whiptail Wallaby, *Macropus parryi*;
Red-necked Wallaby, *Macropus rufogriseus* (also known as Bennett's Wallaby in Tasmania);
Agile Wallaby, *Macropus agilis*;
Swamp Wallaby, *Wallabia bicolor*.

An additional four species may be legally taken where their numbers are in pest proportions. They now generally have a restricted range, but may be locally abundant. They are:

Black-striped Wallaby, *Macropus dorsalis*;
Tamar Wallaby, *Macropus eugenii*;
Red-bellied Pademelon, *Thylogale billardierii*;
Brush-tailed Possum, *Trichosurus vulpecula*.

There are a few limited situations in which wild birds continue to have commercial production value. State law allows parrots to be trapped to supply the domestic avicultural trade, via pet shops. Only the most common species, such as the Galah *Cacatua roseicapilla*, the Sulphur-crested Cockatoo *Cacatua galerita*, the Ringneck Parrot *Barnardius zonarius*, the Long-billed Corella *Cacatua tenuirostris* and the Quorion *Nymphicus hollandicus* are taken. Federal law does not permit live birds to be exported.

In Tasmania, particularly in the Bass Strait islands, approximately 300,000 Muttonbird (*Puffinus tenuirostris*) chicks are taken from their burrows and sold each year. The industry supplies a predominantly domestic market, but a few birds are exported. The season runs in autumn and licensed hunters may take up to 50 birds per day.

There are many other fauna species, such as flying foxes *Pteropus* spp. and the Water Rat *Hydromys chrysogaster*, which could be commercially utilized, but their use is restrained for complex non-scientific reasons.

The wide range of protection between States and species reflects the range in cultural value and community attitudes towards wildlife. Is the fauna resource to be utilized on a sustained basis, are they pests or should they be totally protected? When species are used, there is reticence to take the full value. Often, only skins are retrieved, leaving meat to waste. Some "sport" species are not commercially utilized at all and the many thousands that are shot are left.

There appears to be, nevertheless, general consensus of public attitude that fish can be killed and used commercially on a large scale. The Australian fishing industry has an annual gross value of production of about \$560 million and generates export revenue of a nearly equivalent amount. Although fishing ranks below the major grain and pastoral industries in its contribution to the rural economy, it provides more income and employment than many of the middle ranking farming industries.

The full value of the resources of the Australian Fishing Zone (AFZ) is even greater and includes cultural components:

recreational fishing (which is estimated to generate broad economic benefits significantly larger than commercial fishing);

tourism, particularly in areas such as the Great Barrier Reef region; plus

foreign fishing, which provides licence fees, resource information and development opportunities for Australians; and

traditional fishing, such as carried out by Aboriginal and Torres Strait Islander communities.

There is a continuing public interest in protection and management of marine resources, not only within the AFZ but also in the Southwest Pacific and Indian Ocean regions. Several of the major fish stocks in the AFZ migrate through the fishing zones of neighbouring countries, thus requiring international conservation and management programs.

How well the resources of the AFZ are being conserved and utilized is difficult to assess. Tight controls have been necessary on one major fishery (Southern Bluefin Tuna) in recent years and firm measures taken to control over-exploitation in most other fisheries. Unless stocks are closely monitored and fishing efforts reduced, a number of other stocks and the commercial viability of the industry are clearly at risk. The level of abundance of our main marine species and the economic situation of the industry are the major indices.

The resources of the Australian Fishing Zone are common property and users, including fishermen, endeavour to gain for themselves the maximum share of the available stocks. There is little incentive for individuals to undertake conservation oriented programs. This is in contrast, for example, with farmers who have a strong motivation to protect the resources of their land. Increasingly, there needs to be a framework of legislation, industry/Government consultation arrangements and specific management measures which focus on groups of fishermen, scientists and administrators who have a common interest in protecting and rationally exploiting specific stocks. The northern prawn fishery, for example, has a Parliament-approved management plan and an industry/Commonwealth/State management committee (NORMAC). In addition, each fisherman has been issued with "units of fishing effort" which, while tradeable, provide clearly defined fishing rights.

Formal management plans have also been promulgated for the Torres Strait and Southern Bluefin Tuna fisheries. Plans for the other fisheries are at various stages of development.

The major AFZ fisheries to which this approach should be applied are:

Northern Fisheries

- Northern prawn
- Northern demersal and pelagic
- East coast trawl
- Torres Strait
- Scampi and deepwater lobster
- Pearl shell and Mother of Pearl

Southern Fisheries

- Southeastern trawl
- Southern shark
- Bass Strait scallop
- Southern squid
- Dropline and demersal longline
- Great Australian Bight trawl fishery

Tuna Fisheries

- Southern Bluefin
- East Coast Tuna.

There are a number of fisheries currently managed on advice from the States under Commonwealth and State law which will in future be managed solely by relevant States under the Offshore Constitutional Settlement. These include the Queensland Scallop, Western Australian Snapper, the Rock Lobster and Abalone fisheries.

The long-term conservation management of Australian fish is a serious problem. Under present conditions, most Australian fisheries are overcapitalized and/or overexploited. To ensure longer term viability and economically efficient utilization of the marine resources, total fishing capacity and effort exerted on the resources must be reduced. Financial adjustment assistance is being provided on a fishery-by-fishery basis, subject to those fisheries being properly managed. In 1985, the Commonwealth Government agreed to provide a \$9 million grant over three years, initially to fund a voluntary adjustment scheme in the managed northern prawn industry. In 1986, the Commonwealth Government decided to extend the application of voluntary adjustment programs to other fisheries, conditional upon effective management plans for the relevant fishery and willingness by its fishermen to make a significant contribution to the cost.

There are some fisheries in the AFZ that are not yet developed fully. The identification of these new fisheries and the early introduction of management plans provide the opportunity for diverting some of the excess fishing capacity from existing limited entry fisheries to the new development areas. In doing so, care must be exercised so that the introduction of new technology to reduce operating costs and increase the efficiency of fishing operations does not stress the resource.

In recent years there has been strong interest by foreigners wishing to operate in the AFZ and increasing interest by Australians in joint ventures involving operators for the development of new resources and markets. There also has been interest by Australians in operating in other countries' fishing zones and a strong movement in both the Pacific and Indian Ocean regions for economic development through the exploitation of marine resources for the benefit of coastal States.

Although marine fishing is a form of fauna utilization, economic considerations are uppermost in its management and there are few cultural or aesthetic restrictions imposed. This also applies to other fisheries, inland, game or recreational, but in those cases there is greater awareness of conservation issues. Conflict exists between recreational fishermen and estuarine and beach fisheries based on species such as her-

ring, salmon, mullet or whiting. They are in danger of excessive exploitation. In order to maintain these valuable resources, stringent management practices are also required.

Recreation and Tourism

The recreational value of fauna includes its use in the sports of hunting and fishing, together with other more passive recreational pursuits, such as bushwalking, bird watching and photography. The value lies beyond the immediate act of hunting or taking the photograph. Preparing for and then escaping from everyday activities usually has beneficial effects upon the physical, social and mental state of the participant. Although the effects cannot be measured easily, they are of cultural significance and the opportunity cost of replacing them is significant.

Recreational hunting of birds, particularly waterfowl, is most popular in Victoria and, to a lesser extent, in New South Wales. There are about five times as many hunters in Victoria as in New South Wales (Briggs *et al.*, 1985). The more abundant ducks are the main targets, although there are seasons declared on quail and some other species. The hunted species are:

- Magpie Goose, *Anseranas semipalmata*;
- Water Whistling Duck, *Dendrocygna arcuata*;
- Plumed Whistling Duck, *Dendrocygna eytoni*;
- Mountain Duck, *Tadorna tadornoides*;
- Black Duck, *Anas superciliosa*;
- Grey Teal, *Anas gibberifrons*;
- Chestnut Teal, *Anas castanea*;
- Blue-Winged Shoveler, *Anas rhynchos*;
- Pink-eared Duck, *Malacorhynchus membranaceus*;
- Hardhead, *Aythya australis*;
- Wood Duck, *Chenonetta jubata*.

The Mallard, *Anas platyrhynchos*, also can be hunted. It was introduced to Australia in the mid-19th Century, but did not expand in numbers significantly until the 1950's. Populations mainly occur in a semidomestic situation in city parks and ponds, but have a potentially threatening ability to hybridize with the Black Duck. In New Zealand, mallards have flourished and are now more commonly shot by hunters than the native Black Duck.

Hunting seasons are also declared for:

- Stubble Quail, *Coturnix novazealandiae*;
- Brown Quail, *Coturnix australis*;
- Swamp Quail, *Coturnix ypsilonphora*;
- Muttonbird, *Puffinus tenuirostris*;
- Latham's Snipe, *Gallinago hardwickii*.

Recreational hunting of large mammals is targeted primarily at introduced species such as pigs, rabbits, goats and buffalo. Native species that are hunted for recreation are taken by sportsmen issued with licences for pest control or where species are not protected, such as agile wallabies in the Northern Territory above the 12th parallel of latitude. In Tasmania, recreational open seasons are declared for Red-bellied Pademelon *Thylagale billardierii* and Bennett's Wallaby *Macropus rufogriseus*.

In Tasmania, Victoria and Queensland the following introduced species of mammals are also managed by the wildlife authority for recreation and open seasons are declared and licences issued for:

- Hog Deer, *Axis porcinus* Victoria;
- Sambar, *Cervus unicolor* Victoria;
- Fallow Deer, *Dama dama* Victoria, Tasmania;
- Red Deer*, *Cervus elaphus* Queensland;
- Pheasant, *Phasianus colchicus* Tasmania.

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*Responsibility in Queensland is in the process of transition from National Parks and Wildlife Service to Department of Primary Industries.

The values and attitudes attributable to these introduced species are the same as those given to trout by the inland fisheries authorities. The programs of cultivation and release of young trout are the last vestiges of the activities of the acclimatization societies who conducted so many introductions last century.

Aborigines

In the past, fauna played a valuable part in the culture of Aboriginal Australians, having both direct and indirect value. Today, however, with the few exceptions where Aboriginal communities live in a more traditional manner, the direct value no longer exists. The Aboriginal community is increasingly part of the economy of the rest of the Australian community and is not reliant on traditional sources of "bush tucker" and clothing. Aborigines now make little use of species of mammals, birds and reptiles, though in common with other Australians, they continue to eat fish, especially some marine fish and Crustacea. Nevertheless, their rights under the law to use fauna in a traditional manner remain.

Some Aborigines are reviving the totemic and sacred significance of places and things, including fauna. (The symbol of the kangaroo is, of course, of prime totemic significance for other Australians.) Through activities such as the outstation movement in northern Australia, they are bringing together both their rights under the law and the indirect cultural values, returning to their former lifestyles. Some are moving away from the paternalistic larger settlements to re-establish the smaller traditional family and kinship groups which do use the fauna and, along with the benefit of higher technology, rifles and off-road vehicles.

Prior to white settlement, the impact of the Aboriginal community upon the fauna was profound. They not only preyed heavily upon the fauna using such sophisticated techniques as fish traps and duck nets, but they modified the habitat by burning the grass regularly towards the end of summer as part of their hunting procedures to make passage easier and to harass their enemies (Froggatt, 1913).

CURRENT MANAGEMENT

As a consequence of changing public attitudes, the size of the list of species of fauna which are protected by legislation is growing. The first species on it were individuals protected because of their particular attractive qualities. The process began last century with game animals and song birds. The legislation now covers most native species of terrestrial vertebrates and some species of butterflies and other invertebrates. Consequently, a reverse listing process is often used in legislative definitions of wildlife that identifies species to which total protection does not apply. For example, in the Commonwealth's National Parks and Wildlife Conservation Act 1975 the definition of wildlife is very broad:

animals and plants that are indigenous to Australia;

animals and plants that are indigenous to the Australian coastal sea or sea-bed and subsoil beneath that sea;

animals and plants that are indigenous to the continental shelf of Australia or the super-adjacent waters;

migratory animals that periodically or occasionally visit Australia, the Australian coastal sea or the sea over the continental shelf of Australia; and

animals and plants of a kind introduced into Australia,

directly or indirectly, by Aborigines before the year 1788; and such other animals and plants, not being domesticated animals or cultivated plants, as are prescribed.

Thus, for management purposes and regulations, such wildlife definitions are restricted so as not to include fish or dingoes outside parks and reserves, but they do include marine mammals, reptiles and some amphibians. Similarly, although all native plants are included in such definitions and some aesthetically attractive flowering plants are protected, those used in primary production (such as forest trees) are not protected nor are they the responsibility of the nature conservation authorities.

The management agenda for fauna is currently set by aesthetic values which have a shorter term more political perspective. If ecological values had more influence on fauna policy development and subsequent management, then the long term future of fauna and its conservation would be safer.

Conservation Objectives

There have been many attempts to define conservation. Most of the variation lies in the emphasis placed on the utilization of species. Development of the National Conservation Strategy for Australia (1983) (NCSA) was an attempt to reach consensus. It brought together parties who had a wide range of values for living resource management. They agreed on definitions and established some broad objectives (see Appendix A).

The NCSA has a utilitarian approach and defines conservation of living resources as:

"the management of human use of the biosphere so that it may yield the greatest sustainable benefit to present generations while maintaining its potential to meet the needs and aspirations of future generations".

In the NCSA, conservation thus includes preservation, maintenance, sustainable utilization, restoration and enhancement of the natural environment. Sometimes the preservation and utilization elements of the definition are seen as contradictory, but the priority given to them will depend on factors such as the abundance of the species and its aesthetic appeal.

Fauna Management

A fauna management objective drawn from this conservation definition would be to ensure that species remain widely distributed and in sufficiently large populations to be genetically variable so as to enable their long-term survival. This would be done by managing the species habitat, ecosystems and its populations. This process ought to take place both within reserved land and outside areas, where species can range freely. This is difficult because of the likelihood of conflict with other land-uses.

An early step in management is to determine the size of populations and to measure the distribution and abundance of the species. Techniques in common use are:

spotlight counts from vehicles and on foot;
aerial surveys;

mark, release and estimating the proportion of the population recaptured;

tracking animals that carry radio transmitters;

faecal pellet counts;

counting of sign and footprints in natural areas and specially prepared sand trays;

nest hollow and burrow counts.

Unfortunately, the setting of population goals is rarely, if ever, done on an ecological basis. The aesthetic and economic values discussed in the previous Section are usually the principle management determinant. Such plans and objectives as do exist are imprecise and do not specify goals. For example, plans do not nominate kangaroo population levels as management targets, but they do permit their commercial utilization, albeit controversially. If species are less attractive, over-exploitation occurs before public concern is aroused, for example with some fisheries, such as Bluefin Tuna and prawns.

Wildlife authorities mainly attempt to correct threats posed by the technology of man by preventing killing of species. The effort is directly dependent on the political process. Larger animals with a high cultural value which are regarded as greater assets receive more attention and, hence, funds from wildlife management officers than smaller animals which have lower status. Species which are both large and culturally significant receive the most funds. If species are also pests, such as red and grey kangaroos, they receive most of the conservation and management effort.

One approach to a more scientific process would be to develop a priority index system for management of species. That used by the United States Fisheries and Wildlife Service allocates a degree of threat on a scale one to five. Next, a taxonomic factor is included on a one to 10 scale. The higher the taxonomic category, the higher the score (species are higher than subspecies). An assessment is then attempted of the ecological/socioeconomic value of the species, *i.e.* its popularity rating on a scale 2 to 10. The priority rating is then calculated by multiplying the threat by the sum of taxonomic and ecological factors. Similar processes are used to set priorities for critical habitat.

The most effective technique for managing populations is not prevention of killing, but rather, habitat management. On land in primary production and land dedicated to wildlife conservation, management should aim to maintain prescribed numbers and a wide diversity of different species in the area by maximizing the number of habitat types. Fire frequency and intensity and grazing density are the most effective means of encouraging a mosaic of habitats of differing successional stages. Others include manipulating vegetation by differing stocking rates of domestic animals, logging intensity, slashing and the provision of seed and fertilizer. Where habitat is changing due to land development, it should be quantified. Unfortunately, this is not happening. Nowhere are adequate data being collected on either the changes to habitat or the consequences of such change.

Plans of fauna management should acknowledge the importance of land outside reserves. Although fauna authorities assess the distribution and abundance of populations, the scope for them to manage habitat is usually limited to minor activities in areas under their control, such as reserves and national parks. They are unable to create suitable habitat throughout the range of species. Farmers and graziers should be offered incentives to manage their lands to these ends. Even though maintaining the distribution of native species on lands used for primary production may be economically unpalatable, from a conservation perspective it is essential to the long-term survival of many species. Conservation of a species cannot solely depend on islands of reserved land, but must be based on the necessity for species to range freely. Active management is required throughout the whole of the range of a species, including land tenures.

Where prescribed levels of populations have been determined, techniques for managing them to these ends include restricting movements with fences and electronic devices, removing predators, providing artificial water, shooting and trapping. The variety of traps is large, from small break back traps to large netting enclosures around tanks.

Exploitation

For the economic value of a species to be realized in the longer term, individuals must be harvested on a sustainable basis. This ecological axiom has often been ignored and harvesting rates of many species continue at levels above the ability of the species to renew its numbers.

Some fisheries stocks are declining because of overfishing and changes to the aquatic environment. Estuarine and coastal environments, which are limited valuable resources in Australia and which are highly productive nurseries for aquatic organisms, are being altered for the worse. Many are either contaminated or reduced in area as a result of industrial, agricultural and urban pressures.

Where over-exploitation occurs, management action should first limit the number of operators and their take. In the case of the fishing industry, this means reducing the fishing units. Continued expansion of the fishing boat fleet and greater use of fish-finding technology within the traditional, developed fisheries may result in the eventual depletion of populations to the point where individual stocks fail. The problem is further compounded where people are in the industry on a part-time, semi-professional basis. Constraints should be placed on the entry of additional fishing units into the fishing fleet because of the consequent addition to the total cost of fishing and the increase in competition between fishermen already established. It also places additional costs on government in terms of management and provision of fishing industry facilities, such as jetties and harbours.

The forest products industry is subject to the same criticism of over-exploitation. While this matter is not directly concerned with the exploitation of fauna for commercial purposes, it is relevant because the removal of forests at a greater rate than they are growing obviously has an impact on the long-term survival of the forest fauna. Recent debates about the sustainability of rainforest logging and the decision by the New South Wales Government to halt rainforest operations are a case in point.

Pest Control

Management is more precise for most pest species. The task is to eradicate them, even where they have considerable aesthetic appeal. Humane rabbit eradication is certainly a goal, for example. In general, fauna species that have become established in the wild in 200 years of white settlement are regarded as pests, with the management objective of eradication, providing this can be accomplished without cruelty.

No clear management objectives and plans exist for native species that are pests. The source of controversy over kangaroo culling can be attributed to this key issue. If fundamental objectives were documented in concise, unambiguous terms, the kangaroo debate would largely be defused and a consistent policy and argument could be presented. This is a specific and more visible case of a weakness in management practice which applies generally to all Australian fauna.

In determining the number of kangaroos that should be taken each year, the primary considerations are: the competing claims of the agriculturalists wanting relief from their perceived problem; the needs of the kangaroo industry for a stable supply of products enabling it to keep operating over both good and bad seasons and remain viable so as to respond to pest control requests when needed; and the requests of the kangaroo protection organizations to minimize the numbers of kangaroos killed. Governments have difficulty in simultaneously satisfying these divergent demands. Existing policies have been developed in a reactive rather than creative manner in an attempt to compromise competing

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interests. Although there is little biology in this procedure, extensive aerial surveys have been conducted and there is no doubt that the proportion of the population taken is well within the sustainable harvest. Ironically, the debate does not take place in the context of changes in the animals' habitat, the one factor that has the long-term capability of adversely altering populations.

One of the problems in determining if species really are pests is that generalized control mechanisms, such as commercial hunting, are put in place on a broad scale, whereas the agricultural damage is often localized in both time and place. Kangaroos are taken all year and over a large area, but they are only pests in local circumstances. For example, when wheat is young and apparently succulent, large numbers of grey and red kangaroos can be counted emerging from forest and grazing lands nearby (Hill, *et al.*, in press). In times of drought, kangaroos undoubtedly do compete with domestic stock for remnant pastures and water. They prefer to go through, rather than over, fences and can thus severely compromise attempts by graziers to fence other pests out of their lands.

Surprisingly, in view of the acrimony of debate over kangaroo conservation, there is substantial agreement in the community on many aspects of kangaroo management. Most groups would not dispute that the overall goal for kangaroo conservation is to ensure that kangaroos continue to be widely distributed in sufficiently large populations to ensure long-term survival, that control techniques should not be cruel and that only competent people should be permitted to kill kangaroos. Fencing is also seen as a very useful means of preventing pest damage. The maintenance of national parks and sanctuaries in which shooting is not allowed is not disputed. Points of criticism, both here and overseas, include the numbers of kangaroos killed, methods and estimates of populations, cruelty, the morality of killing wild animals, the ethics of making money from wildlife and shooting by non-commercial "sportsmen".

Topics rarely raised are the long-term objectives of kangaroo management, the strategy for achieving the objectives, the actions for implementing the strategy, the consequences of banning commercial shooting, alternatives for reducing the pest status of kangaroos and the priority for kangaroo conservation versus the conservation of other species.

Other components of the debate lead to strong disagreement and reflect unaddressed management objectives. Should kangaroo populations increase or decrease and what is the desirable kangaroo population for the whole of Australia and for a given region? (The answer is essential if a defensible figure is to be set on the numbers to be killed). What numbers of kangaroos should be taken before and after a drought? Where kangaroos are killed as pests, should more be taken from the population than are capable of being replaced in a year?

Decisions based on measurable objectives are needed: which populations of kangaroos are too dense and need to be reduced; which populations (if any) can be exploited on a sustainable yield; and which populations are too small and need to be increased by intensive management. Once these points have been established, the larger question of whether kangaroos are agricultural pests can be addressed. Australian pastoralists should be encouraged to view kangaroos as a resource instead of regarding them as pests, since they have the potential to complement current commercial grazing animals. Kangaroos could be the better grazing animals for much of Australian rangelands, in the longer term. They evolved here and are probably better adapted to survive here than sheep or cattle. Kangaroos also appear to have far less deleterious effects on Australian native pastures and soils and their numbers fluctuate with good and bad seasons rather

than destroying the food resource. The meat is low in fat and cholesterol, which makes it attractive to health-conscious consumers.

Introductions and Naturalizations

The extent of, and reasons for, introductions to the Australian fauna are the subject of another Chapter in this Volume (see Chapter 10).

The impact of introduced animals on the Australian environment and fauna has not stabilized and many (*e.g.*, *Bufo marinus*) continue to spread into suitable habitats, although fluctuations in their populations are dependent on seasonal conditions. The introduction of myxomatosis led to some reduction in the density of rabbit populations, but control measures against other feral species have been largely ineffective, except when applied locally and intensively. Failing the discovery of new and effective means of control, such as poisons or species-specific diseases, we apparently shall have to accept the introduced species as part of the Australian fauna.

To avoid a recurrence of past errors, there is the necessity to ensure that further introductions do not occur. Legislative restrictions on the importation of exotic species under the Quarantine Act 1908 are concerned primarily with the protection of livestock from exotic diseases and the restriction of exotic species within the security of well-managed zoos. The Wildlife Protection (Regulation of Imports and Exports) Act 1982 restricts imports of foreign species on environmental grounds. Control is not perfect. A recent threat arose when gerbils and Mongolian hamsters were introduced and bred in a large number of pet shops. They are prolific, arid-adapted, granivorous rodents which could become a major pest in the drier grain growing areas of Australia.

Impact on Veterinary Science and Medicine

The fauna has had little direct economic impact on medical and veterinary science (the same cannot be said for the Australian flora). With a few exceptions, the Australian fauna has not provided material either for application for treatment or as an origin of infectious agents of diseases that are important to human or domestic animal health.

Indeed, at the time of white settlement Australia was free of many infectious agents of domestic stock that are common in other parts of the world. The Australia fauna did not have any ungulates, Artiodactyla and Perissodactyla, and consequently was free of their diseases. This assisted the invasion of Australia by hooved animals, both domesticated and feral. In Africa, diseases such as rinderpest placed limits on the lands which could be colonized for the rearing of livestock.

With the possible exception of birds, the components of fauna generally do not appear to be likely reservoirs of infection following the introduction of an exotic disease. Wild birds have been implicated as the source of the causative infectious agent in many outbreaks throughout the world. They are believed responsible for a 1976 outbreak of Avian Influenza in Victoria (Downie *et al.*, 1977), the 1983 outbreak in Pennsylvania (Webster, 1984) and probably were connected with the 1985 emergency in Victoria (Forman *et al.*, 1986).

Quarantine prohibitions on bird imports into Australia are primarily designed to protect the poultry industry by keeping out exotic diseases such as Avian Influenza or virulent Newcastle Disease. Yet every year thousands of birds enter as free-flying migrants and are constantly introducing new strains of both Avian Influenza and paramyxo viruses

(Newcastle Disease) into local avifauna. The infectious agents are most frequently found in ducks, probably due to the ease of transmission in water.

Although strains from migration rarely cause illness in wild birds, they can be virulent in domestic poultry. In the case of Newcastle Disease, the greatest risk for Australia is not bird migration, but disease due to smuggled eggs and birds. Surveys in Western Australia of more than 8,000 birds from 117 avian species have yielded 110 viruses. Of these, 27 have been identified as Newcastle Disease and 49 have been typed as influenza (Mackenzie, 1984). Avian Influenza has also been isolated from a trans-equatorial migrant shortly after first arriving in Australia. Waders approaching Australia may stop in Indonesia or Papua New Guinea to replace their fat deposits before resuming their flight.

The same viral strain as occurred in the 1976 Victorian outbreak in poultry was found in a shearwater off the Queensland coast, but a causal relationship has not been proved. Similarly, the strain that caused the massive outbreak in Pennsylvania in 1983-84 has been found in wild birds.

The migration route for the introduction of Avian Influenza and Newcastle Disease cannot be prevented. Nor can the viruses be eradicated from native birds. One practical contribution in addressing the threat, however, is to monitor the geographical and species distribution of any infection. Samples need to be taken from wild birds and introduced species such as starlings and pigeons, which are in closest contact with domestic poultry.

Indigenous helminth parasites carried by the fauna are generally incapable of infecting domestic stock. An exception is the hydatid, *Echinococcus granulosus*, probably carried by macropodids and dingoes (Kumaratilake & Thompson, 1984) which has medical importance as a source of reinfection. The wild cycle diminishes the effectiveness of public health control programs by constantly reinfecting areas that are intended to be hydatid-free and have a lower human health risk. A similar situation has arisen in Tasmania where Sheep Liver Fluke, *Fasciola hepatica*, is carried by red-necked wallabies (McManus, 1979).

In the past, however, diseases of livestock appear to have been important for fauna. There is circumstantial evidence that pathogens introduced by the settlers with their livestock and other animals have had a profound adverse impact upon fauna. Epidemics are said to have affected native species and the occurrence of isolated pockets of species on islands of habitat supports this interpretation. Where epizootics do occur, the cause is likely to be a combination of stress due to changing habitat, pressure on food resources and the presence of a new pathogenic agent.

In summary, despite the paucity of survey work done, one may generalize that Australian faunal diseases are not important in the economy of domestic livestock and overall livestock diseases are not important in the management of fauna.

Other legislation protects the habitat of fauna as part of the conservation area network of national parks and nature reserves. The purpose is to protect ecosystems and ecological processes. The approach is limited, however, because legislation fails to protect the habitat of species outside reserves. Details of legislation are given in Appendix B.

A recent non-legislative development is the production of codes of practice for the humane treatment of animals, for example the code on kangaroo shooting. Unfortunately, they are incapable of providing detailed guidelines for all the circumstances which may apply to persons wanting to destroy pests or conduct research on captured animals. They aim to lay down the principles that should guide the operator or hunter in his choice of methods and draw attention to matters that must be considered before field work commences.

Legal authority for fauna (and land use) is vested in the State and Territory Governments, each with its own authority whose prime responsibility is the conservation and management of fauna within its boundaries (including the Commonwealth where it controls a Territory). This occurs because the Australian Constitution gives specific legislative powers to the Commonwealth and the residue of unspecified powers resides with the States. At the time of Federation in 1901, fauna was not the national issue it is today. Nevertheless, the Commonwealth controls the export of fauna, is responsible for fauna matters which might flow from international treaties, such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and encourages the development of national policies on fauna through cooperative activity with the States.

The notion that governments are responsible for fauna and the State ownership concept follows the tradition of English law and Magna Carta, in which fauna is the property of the Crown. The fauna becomes the property of the landholder only when reduced to possession, when taken by legal hunting, for example. This principle is put into effect by State fauna legislation, protecting all native fauna from being killed until they are taken and hunted under licence. Sometimes the licence is defence of life and limb or on the basis of mitigating agricultural damage. In some States, hunting is allowed where species are in excess numbers and hunting would ensure satisfactory survival. There is also legal variation between States over whether species can be shot for sporting purposes or can be used commercially. In all States licences also may be issued for special purposes such as research and scientific investigation, although they are difficult to obtain for endangered species.

Recently, the Commonwealth has increasingly legislated on conservation and fauna matters, using the authority of powers granted to it either directly or indirectly by the Constitution. It has relied on its interests as the national government, the power with respect to international and interstate trade and commerce, external affairs, trading corporations, defence, territories of the Commonwealth, taxation, quarantine, places owned or acquired by the Commonwealth and granting financial assistance directly to State Governments. The use of the external affairs power to influence decisions within States is particularly controversial and has been the subject of dissent between the States and the Commonwealth. A list of conventions of significance in Fauna Conservation is given in Appendix C.

Some States have seen the Commonwealth extending its authority and claiming powers which were not intended by the writers of the Australian Constitution. A notable case concerned the prevention of the construction of the Gordon-below-Franklin Dam in Tasmania by the use of the Convention for the Protection of the World Cultural and Natural Heritage. The Commonwealth enacted regulations under the

LEGISLATION

Fauna legislation has the general nature of preventing killing, holding or interfering with most native fauna except under licence. Fines are imposed for contravention of these provisions. Special fines are allocated to further protect endangered species. Provision is made for specimens to be taken or killed under licence for a variety of purposes, such as scientific investigation, pest control and sport hunting. The taking of non-native fauna and other wildlife is regulated under a variety of other laws, including those that apply to fisheries management.

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National Parks and Wildlife Act 1975 to give effect to the provisions of the Convention. The World Heritage Properties Conservation Act 1983 was passed to provide for the protection of certain property that Australia has identified as natural heritage or cultural heritage within the meaning of the Convention. Both pieces of legislation were examined by the High Court and the power of the Commonwealth was upheld.

The ability of States to manage their fauna has also been affected through interpretations given to Section 92 of the Constitution, which guarantees free trade between States. The issue is whether State wildlife authorities have the ability to place controls on the movement of items such as caged birds and kangaroo skins across State borders. The fauna authorities claim that such restrictions are an integral part of their fauna management programs, whereas the less scrupulous dealers use the provisions of the Constitution to circumvent State law designed to protect fauna.

One solution to the interstate trade problem is for State laws to be similar, so there are no differences of protection status between States for dealers to exploit. There is resistance, however, to such uniformity of legislation because some States see it as an erosion of their right to be different and of the need for legislation to reflect regional differences. One argument, for example, is that States which do not allow the trapping of birds or the commercial killing of kangaroos have no need to have in place all the trading regulations and machinery to protect such wildlife interstate.

Discussion between the Commonwealth and the States on these and other matters is facilitated by the Council of Nature Conservation Ministers (CONCOM). The Council was established in 1974 and provides a forum for consultation on matters relating to nature conservation and wildlife protection. CONCOM is supported by a Standing Committee of officials nominated by the respective ministers. Sub-committees known as *ad hoc* working groups deal with specific matters such as kangaroo management, endangered flora and fauna, law enforcement, education and training and the implementation of international agreements concerning migratory birds.

Fisheries jurisdiction in Australia is also divided between the Federal and State Governments, but on a different basis. Broadly, the States/Territories administer marine fisheries to the three nautical mile limit and the Commonwealth is responsible from three miles to the 200 nautical mile limit. Under relevant provisions of the Offshore Constitutional Settlement (OCS) between them, however, the governments have agreed to develop more flexible fisheries jurisdiction arrangements within the AFZ.

Consultation and cooperation between the States and the Commonwealth on fisheries matters have traditionally been achieved within the framework of the Australian Fisheries Council, Standing Committee on Fisheries and their sub-committees. In recent years, joint industry/Commonwealth/State management advisory committees and the Fishing Industry Policy Council of Australia have provided advice on the management of specific major fisheries.

Other ministerial councils, such as the Australian Agricultural Council and the Australian Forestry Council, also deal with matters which relate to the conservation and management of Australian fauna and have sub-committed structures. Of particular relevance to native fauna is the Vertebrate Pests Committee (VPC) of the Standing Committee on Agriculture. Its main task is to protect Australian agriculture and the environment from introduced vertebrate pests. The committee undertakes a continuing review of the established vertebrate pests in Australia with particular reference to their control or eradication and to measures for the exclusion of potential pests from overseas.

The State Exotic Animal Disease Acts and the Commonwealth Agricultural Quarantine Bill aim to prevent the transmission of introduced diseases and make provision for plans and procedures for their control. The VPC is helping to do this by developing joint coordinated plans and strategies to reduce populations of feral animals in areas of greatest risk from exotic diseases and by testing plans to eradicate susceptible feral and native animals from infected areas in exotic disease outbreaks. There may be aspects of the vertebrate pest control plans that would apply in the event of an exotic disease outbreak which would affect native fauna. Not that the mammal fauna represents a great threat; most concern about exotic disease control should be expressed in the reverse direction, *i.e.* to ensure that control procedures do not have unnecessary effects on non-target species. The purpose of the plan is to reduce the size of economic loss which would follow an outbreak of exotic disease in livestock; to reduce agricultural production losses caused by vertebrate pests and to help protect the environment.

THE FUTURE

In the current free-market economic milieu, landholders and others who greatly affect fauna are encouraged to increase productivity and alter the natural environment. This is done by incentives to greater capitalization such as by depreciation schedules, taxation policies and many other financial forces. As a result, more natural resources are consumed and mechanization becomes more widespread, but the long-term consequences for sustainability and fauna conservation are not part of the equation. Producers often over-exploit the resource after having been encouraged to obtain bigger boats, more sophisticated fishing technology, forest pickers and cane-cutting machines or by overstocking in droughts and broad acre farming of marginal land.

This highlights the inconsistency between continuous growth in human population and *per capita* demand and maintenance of essential ecological processes and life support systems. The National Conservation Strategy for Australia (NCSA) drew attention to this, but unfortunately does not suggest how to tackle the problem. Under current economic planning, the market is the supreme policy determinant and there is an economic imperative for continued growth in production, with little scientific assessment of the biological ability of living resources to produce in the long term.

To correct this, there needs to be a strategy for the land and rural economy that can be integrated with general economic policy, supported and adopted by all departments, governments and sectors of the community. The need is for a macro-perspective. Fauna management should be part of resource management. Current public attitudes mainly concentrate on short-term local and aesthetic issues and, consequently, no time is allocated to how many micro-observations can be integrated to a broader perspective. Instead of encouraging the population and the consumer demand to increase without question, economic policy makers need to be much more aware of ecological limitations to living resource production.

The adoption of a holistic perspective and a multidisciplinary approach to resource and land-use management is very difficult. It has not been satisfactorily achieved so far because it involves resolving many competing interests. State and local governments are responsible for land-use matters and at the Commonwealth level several departments have an indirect interest, but no level of government has a satisfactory or efficient means of coordination. Economic planning decisions for which the Commonwealth is responsible are probably the

most effective. They have potential for an effective and comprehensive means for influencing land-use and resource management practice.

Successfully advocating a multidisciplinary approach is a task for a senior authority following a high level commitment to proceed to implementation.

The agenda for the development of such plans should start with the determination of National Goals which set down long-term overall intents or national aspirations. They would give a reference against which to measure progress. Those proposed by the Australian Science and Technology Council (ASTEC) might serve as the basis for discussion:

security — safety against external attack, protection against natural disasters;

prosperity — a stable or rising standard of living, subject to variations according to effort and capacity, but with systematic support for those who, for various reasons, might otherwise live in poverty;

social cohesion — a harmonious society without cleavage along ethnic, religious or class lines, and with provisions for peaceful change in policies and institutions;

community welfare — provision for community health both mental and physical, care of the disadvantaged and disabled, opportunity for educational achievement;

cultural and scientific advance — a high quality of creative effort in the arts, sciences and technologies and a wider understanding of them.

There next needs to be a set of long term objectives which are specific statements of what is to be achieved by certain dates. They should be quantified in most cases so as to be subject to measurement and evaluation. The overall objective would be to promote a pattern of resource use which reflects availability. Specific goals would be growth targets for the economy without increased consumption of non-renewable resources, population levels for living resources (including fauna) that improve their quality or quantity and reverse past errors, stable or decreasing national human population, the nomination of an acceptable unemployment level and encouragement for technology to perform boring, repetitive tasks.

Taxes, which have such broad effects on land-use and resource management, are a potential tool for much needed national action plans on population stabilization, resource conservation and living resource management. Changes in

taxation should be developed by the supreme government bodies and integrated as vitally important aspects of economic policy. The task is to integrate conservation and development and to emphasize their interdependence and common ground. Pursuing the objective of a more biologically realistic basis for the economy could also lead to royalties and probate being imposed to reflect the limited availability of such natural resources as land, water, minerals, forests and fauna. Income tax could be reduced to enable people to spend their income to employ other people, an abundant resource.

SUMMARY

The standards and sophistication of fauna management vary greatly between fauna species and areas. Monitoring of populations of some species, such as the large kangaroos, is proceeding at quite a sophisticated level using extensive aerial surveys. Other species are largely ignored. Nowhere, however, are adequate measures being made of the changes to habitat or the consequences of such change. Even for the abundant species that are so common that they are used commercially, it is essential not only to assess the resource and determine an annual cull, but also to measure changes to the refuge areas and other components of the environment essential to reproduction of the animal.

Because plans of management for fauna, where they exist, do not contain sufficient detail, short-term objectives are illogical and largely based on aesthetic and current cultural values. Species such as kangaroos are at the one time pests, the subject of a harvest which is said to be sustainable and the object of major cultural attention with implicit (and often explicit) demands for total protection. Until there is a wider debate and objectives are set in the context of economic development, changing habitat and land-use, conservation management and legislation will continue to be *ad hoc* and confused. Objectives must be framed in advance and the desired density, distribution and economic use that we wish for species of fauna described with precision.

We must also face the fundamental ecological dilemma of how to integrate the needs of an expanding human population, the current imperative of community expectations for an economy which can improve living standards and the reality of limited natural resources. Otherwise the fauna will not be conserved.

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APPENDIX A — CONSERVATION STRATEGY

CONTENTS OF THE NATIONAL CONSERVATION STRATEGY OF AUSTRALIA

The NCSA identifies the broad ecological problems facing resource management in Australia and puts them in perspective with one another. These are the matters for which urgent solutions are needed. They are based on the three main objectives of living resource conservation identified in the World Conservation Strategy and which have also been adopted for the NCSA:

to maintain essential ecological processes and life support systems on which human survival and development depend;

to preserve genetic diversity on which depend the breeding programs necessary for the protection and improvement of cultivated plants and domesticated animals, as well as much scientific advance, technical innovation and the security of the many industries that use living resources; and

to ensure the sustainable utilization of species and ecosystems which support millions of rural communities as well as major industries.

An additional objective, which has been adopted for the Australian strategy, is:

to maintain and enhance environmental qualities which make the earth a pleasant place to live and which meet aesthetic and recreational needs.

The Strategy nominates obstacles to achieving these NCSA objectives and states that doing something about them is a matter of urgency.

The main contribution made by the Strategy so far has been to obtain wider recognition of the importance of the ecological relationship between land-use and ecosystems. The strategy emphasizes many times that decisions taken in one area affect others. It notes the need for planning which has an ecological approach, for improved coordination between the various bodies involved in making decisions about living resources and for more certainty about which of the local, state and federal levels of decision-making is appropriate for particular matters.

The Strategy particularly recognizes the urgency of soil conservation, but is not very specific about what should be done or who should do it. The Strategy notes that soil erosion is largely the result of inappropriate use and management of land, that soil erosion degrades dams and waterways, adversely affects terrestrial and aquatic ecosystems and community facilities and poses a major threat to agriculture and the Australian economy. Included as a Priority National Requirement is the need to ensure that land management practices are consistent with the long term productivity of living resources and that degraded and eroded lands are restored.

The Strategy continues in a similar vein by noting the limitations for development created by the quantity and location of water in Australia. Some river systems, wetlands and underground water resources are severely degraded and water and soil salinity are now widespread problems. Clearing for agriculture, grazing and urban development has exacerbated this situation and destroyed much of Australia's native vegetation.

APPENDIX B — FAUNA LEGISLATION

COMMONWEALTH

National Parks & Wildlife Conservation Act 1975. The Australian National Parks and Wildlife Service is established under this Act. It provides for the establishment and management of national and other parks and reserves in Australia and for the protection and conservation of wildlife.

Wildlife Protection (Regulation of Exports and Imports) Act 1982. Regulates the import and export of certain animals, plants and goods. With a few specified exceptions, the Act does not ban commercial trade, but rather seeks to prevent over-exploitation and other threats to the world's wildlife. It does so through a system of permits (for individual transactions) and authorities (for multiple exports or imports). Schedules to the Act list wildlife to which strict export and import controls apply. Currently, they comprise the following categories:

Schedule 1. Appendix I to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) – except cetaceans.

The official list of Australian endangered vertebrate fauna endorsed by the Council of Nature Conservation Ministers (CONCOM).

Birds listed in the Agreement between the Government of Australia and the Government of Japan for the Protection of Migratory Birds and Birds in Danger of Extinction and their Environment.

Schedule 2. Appendix II to CITES – except cetaceans.

Schedule 3. All species of the mammalian order Cetacea (whales, dolphins and porpoises).

Schedule 4. Lists Australian native animals and plants to which export controls do not apply.

Schedule 5 & 6. Lists live animals and plants to which import controls do not apply.

Schedule 7. Lists Australian native animals that may be exported as the household pets of departing Australian residents.

Schedule 8. Consists of the text of CITES treaty.

Whale Protection Act 1980. Prohibits the killing, injuring, taking or interfering with any cetacean (whale, dolphin or porpoise) in waters of the Australian Fishing Zone. Administered in consultation with States and Northern Territory.

Fisheries Act 1952 (as amended) plus several related Acts. Regulates the taking of fish from Australian waters by a licensing system. Fishing in specified areas may be prohibited. Amendments and supplementary legislation enable preparation and publication of plans of management for particular fisheries.

Continental Shelf (Living Natural Resources) Act 1968. Regulates, by a system of permits, the taking of sedentary organisms from the Australian continental shelf.

Australian Heritage Commission Act 1975. Establishes the Australian Heritage Commission and provides for the protection at the federal level of aspects of the natural environment which potentially includes fauna.

Great Barrier Reef Marine Park Act 1975. Provides for the establishment of the Great Barrier Reef Marine Park and authorizes the making of regulations specifically regulating or prohibiting acts whether in the Marine Park or elsewhere that may pollute water in a manner harmful to animals in the Marine Park.

Antarctic Marine Living Resources Conservation Act 1981. Gives effect to Australia's obligation under the Convention of the Conservation of Antarctic Marine Living Resources. Under the Act all species of living marine organisms are protected by the imposition of a permit system.

States Grants (Nature Conservation) Act 1974. Provides for financial assistance to the States for purposes connected with nature conservation.

Quarantine Act 1908 and the new Agricultural Quarantine Bill. Contain measures for the prevention of the introduction or spread of diseases or pests affecting man, animals or plants.

Income Assessment Act 1936. Makes tax concessions available to primary producers who incur expenditure on conservation measures such as pest control.

NEW SOUTH WALES

National Parks & Wildlife Service Act 1974. Provides for the Service to establish, manage and preserve national parks, nature reserves, game reserves historic sites and certain fauna, native plants and Aboriginal relics.

Pastures Protection Act 1934. Establishes Pastures Protection Boards. Noxious wild animals must be continually suppressed. Control officers have the right of entry to conduct control work and destroy harborage.

VICTORIA

Wildlife Act 1975. Aims to protect all wildlife for varied and future needs. Provides for establishment of three types of reserves: State Game Reserves, State Game Refuges and State Faunal Reserves. Enables Wildlife Management Cooperative Areas to be set up, on private land or on Crown land vested in other authorities, and a plan of management prepared. Mining in reserves requires the prior approval of the Minister for Conservation, Forests and Lands.

National Parks Act 1975. Outlines scope and policies of National Park Service and provides for national park management and development of different types of national parks.

Land Protection Bill. When passed will supersede **Vermin and Noxious Weeds Act 1958.** Provides for land protection in Victoria including pest animals, weeds and soil conservation.

QUEENSLAND

National Park and Wildlife Act 1975–1982. Establishes the office of the Director of National Parks and Wildlife to administer statutes relevant to the conservation of flora, fauna and natural landscape with provisions and powers, controls and penalties to regulate public activity in the interests of nature conservation.

Rural Lands Protection Act 1985. Provides for the destruction of vermin and noxious plants. Land holders and authorities are given certain duties in relation to controlling vermin. The Rural Lands Protection Board is formed to advise the Minister with regard to the Act's operation.

SOUTH AUSTRALIA

National Parks and Wildlife Act 1972. Provides for the conservation of wildlife in a natural environment; the control of fauna outside reserve areas; and the establishment of and management of reserves for public benefit and enjoyment.

Animal and Plant Control Act 1986. Establishes Animal and Plant Control Commission for control of animal and plant pests for protection of agriculture, environment and public safety.

WESTERN AUSTRALIA

Agriculture Protection Board Act 1950. Creates the Board and defines its powers.

Wildlife Conservation Act 1950–1980 as amended. Protects native flora and fauna and manages the harvesting of those species subject to exploitation.

Agriculture and Related Resources Protection Act 1976–1983. Regulates the introduction, spread and keeping of certain plants and animals with the object of protecting primary industries and the resources related to primary industries.

Conservation and Land Management Act 1984. Provides for use, protection and management of public lands, water, flora and fauna. Establishes the Land and Forests Commission and the National Parks and Nature Conservation Authority which have advisory functions.

TASMANIA

Vermin Destruction Act 1950.

National Parks and Wildlife Act 1970.

NORTHERN TERRITORY

Territory Parks and Wildlife Conservation Act 1977–1984. Deals with control and regulation of wildlife and administration of parks reserves and sanctuaries.

AUSTRALIAN CAPITAL TERRITORY

Nature Conservation Ordinance 1980.

APPENDIX C — TREATIES AND INTERNATIONAL CONVENTIONS THAT AFFECT FAUNA MANAGEMENT

Treaties to which Australia is party concentrate on protection of species and, in some cases, their habitats. Australia is a contracting Party to the following:

(1) **The Convention on Wetlands of International Importance Especially as Waterfowl Habitat** concluded on 2 February 1971 at Ramsar, Iran. Australia signed the Convention on 8 May 1974. Contracting parties are obliged to endeavour, through management, to increase waterfowl populations on appropriate wetlands. The Convention further aims to promote the conservation of wetlands and waterfowl, to establish nature reserves on wetlands and to provide adequate protection and wardening of wetland reserves; and to promote training of personnel competent in wetland research, management and wardening.

There are now 28 Australian wetlands on the list of Wetlands of International Importance maintained under the Convention. There are two in the Northern Territory, 10 in Tasmania, 10 in Victoria, three in New South Wales and three in South Australia.

The List now comprises 344 nominations totalling 1.98 million ha around the world. Australia currently rates third amongst the Parties to the Convention in the number of nominated wetlands and fourth in terms of the area covered by nominations.

The second Conference of Parties to the Convention, held at Gröningen, the Netherlands, in May 1984, adopted a number of "Action Points for Priority Attention" which the Council of Nature Conservation Ministers (CONCOM) has now endorsed for incorporation into existing wetland management programs.

(2) **The Convention Concerning the Protection of the World Cultural and Natural Heritage** was concluded on 16 November 1972 and was ratified by Australia on 22 August 1974. The Convention requires that *inter alia*, parties protect their natural heritage including the habitat of threatened species. The Convention came into force on 19 December 1975. Australia meets her obligations under the Convention in part through the Australian Heritage Commission and through Regulations under the NPWC Act 1975 which lists the Convention in a schedule.

The World Heritage List established under the Convention includes Kakadu National Park, the Great Barrier Reef, the Willandra Lakes Region, Lord Howe Island, the Franklin-Lower Gordon Wild Rivers National Park, the South-West National Park, the Cradle Mountain-Lake St Clare National Park and the rainforests of New South Wales. These include populations of endangered and vulnerable species of Fauna.

(3) **The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)** was concluded at Washington on 3 March 1973 and entered into force in Australia on 27 October 1976. Parties to this Convention regulate trade in nominated species of fauna and flora threatened with extinction and other nominated species which could become threatened by uncontrolled trade. Regulations

pertaining to this Convention were first made under the Customs Act 1901 and the various External Territories Acceptance Acts.

Since that time, Australia has been seen internationally as having taken an important role in the continued development of CITES by supporting strong conservation measures for species threatened with extinction but also allowing for the rational utilization of wildlife resources where this does not jeopardize the survival of the species in the wild. This approach is reflected by enabling legislation, the Wildlife Protection (Regulation of Exports and Imports) Act 1982, which came into force in 1984.

Meetings of the Conference of Parties to CITES are held biennially to discuss ongoing implementation of the Convention. Listings of the various categories of species at risk are reviewed by the CONCOM *Ad Hoc* Working Group on Endangered Fauna, although none of the Australian endangered species is endangered by excessive international trade. Australian imports of wildlife have been of little consequence to overseas endangered species. Australian quarantine laws already prevented the import of living animals such as South American parrots while the market for fur products is small in the Australian climate. Nevertheless, the Australian trade in reptile skins and ivory would be larger than it is without the restrictions of CITES.

(4) **The Agreement between the Government of Australia and the Government of Japan for the Protection of Migratory Birds and Birds in Danger of Extinction and Their Environment** came into force on 30 April 1981. The Agreement was signed in Tokyo on 6 February 1974.

Although the primary objective of the Agreement is cooperation between the Governments of Australia and Japan to protect species of birds that migrate between Australia and Japan, a further objective is for each government to take steps to preserve species or subspecies of birds in danger of extinction.

Implementation of the agreement in Australia is promoted through the CONCOM Working Group on International Agreements Relating to Migratory and Wetlands Birds.

Officers including those of the Tasmanian National Parks and Wildlife Service have visited Japan as part of a cooperative survey of Latham's Snipe, *Gallinago hardwickii*, on its breeding grounds in Japan.

In an exchange of diplomatic notes during February 1985, the Japanese and Australian Governments agreed to add 10 species to and remove one from the Annex to the Agreement, which lists the migratory species now covered by the Agreement. Seventy-six species of migratory birds are now listed.

(5) **The Convention on Nature Conservation in the South Pacific** was adopted at Apia, Western Samoa on 12 June 1976. This convention aims to establish a broad framework for nature conservation in the South Pacific Region. Australia participated in the meeting which drafted the Convention and was one of the countries which signed the agreed text. The Convention refers in particular to the conservation of

endangered species and measures to protect them. Assurances have been sought by the Commonwealth from the States on legislative and executive action to allow Australia to ratify the Convention.

(6) The **Agreed Measures for the Conservation of Antarctic Flora and Fauna** were concluded at the third Antarctic Treaty Consultative Meeting, held at Brussels on 2–13 June 1964. The Agreed Measures establish a system for protection of wildlife and its habitats in Antarctica, and will come into effect when adopted by all consultative parties. The Antarctic Treaty (Environment Protection) Act 1980 enables Australia to adopt the measures.

(7) The **Antarctic Marine Living Resources Convention** concluded at Canberra, on 20 June 1980, establishes the principles (including conservation) which are to apply to all harvesting in the seas south of the Antarctic Convergence. It provides for the maintenance of all ecological relationships and aims to prevent irreversible changes to the ecosystem or its component populations. An international commission, based in Hobart, has responsibility for drawing up measures to conserve all creatures within the ecosystem.

The Antarctic Marine Living Resources Convention Act 1981 supports the Convention. The main provisions of the Act will come into operation when the Convention comes into force internationally.

(8) The **Convention for the Conservation of Antarctic Seals** came into force in March 1978; it applies to seas and ice-flows south of 60°S latitude. It aims to promote and achieve the protection and scientific study of Antarctic seals, while making provision for their rational use as resources. Australia has signed the Convention, but ratification is pending appropriate legislation. The issue of the commercial use of seals has been controversial.

(9) The **International Convention for the Regulation of Whaling**. This Convention, to which Australia is an original signatory, came into force in 1946. The Convention established the International Whaling Commission (IWC). The Convention was supported successively by the Whaling Acts of 1935, 1948 and 1960. The last was repealed by the Whale Protection Act 1980. The Australian policy of seeking a worldwide ban on whaling and protection for all cetaceans is pursued internationally through the IWC. In 1982, the Commission agreed to a moratorium on commercial whaling to commence in 1986. The decision to suspend commercial whaling represented the culmination of years of effort by conservation-minded governments and non-government conservation groups. Some whaling has continued during the period of the moratorium under objection (Japan, U.S.S.R. and Norway) and under national scientific permits (Iceland and Republic of Korea).

12A. CLASSIFICATION AND NOMENCLATURE

H. G. COGGER

INTRODUCTION

As many as 30 million kinds (species) of animals have been estimated to inhabit planet Earth, of which fewer than 1.5 million have been described formally and classified by zoologists. New species are described at the rate of about 5,000 per year (Ehrenfeld, 1986).

The classification of objects in their environment — be it animals, mountains or gods — is an intrinsic activity of the human mind. It represents a means of organizing information and maximizing its utility by bringing together in groups those objects with certain features in common. With the development of language, effective communication between two or more individuals called for the assignment of definitions and names to the various categories in any given classification so that its utility could be shared with others. Every day each of us classifies objects, thoughts or feelings and each of us uses classifications. These may be classifications which we devise ourselves (such as separating the people we meet into discrete groups: close friends vs. casual acquaintances; family vs. non-family; males vs. females) or they may be classifications devised by others (such as those which define people by their jobs as policemen, politicians, public servants, scientists, dentists). About half the words in any dictionary represent objects or concepts in a classification.

Classification may be defined as the assignment of people, things, animals, ideas, etc. which possess similar qualities or characteristics to groups or classes.

Classifications and the processes of classifying pervade contemporary society. Entire bureaucracies are established by governments and private agencies to classify people and objects. Such classifications may have benign objectives (e.g. to identify and support the elderly and infirm) or sinister ones (e.g. to identify and inactivate internal opponents of a political system).

The process of identifying, describing, classifying and naming animals is known as zoological taxonomy. It is one of the major components of the broader field of zoological systematics: the study of the diversity, origins and relationships of animals.

Of course, the levels of taxonomic knowledge and research vary widely from one animal group to another, from one geographic region to another and from one biotope to another. Thus, about 97% of the world's 4,000 species of mammals have been discovered and described whereas less than 20% of the world's estimated insect fauna are known. This taxonomic disparity is exacerbated by regional differences in the distribution of people and taxonomists: the insects of Europe are much better known than those of New Guinea and those of temperate grasslands are much better known than those of equatorial forests.

Do such gaps in taxonomic knowledge matter? Unfortunately they do! The world-wide rate of environmental change and degradation during the past 30 years has increased to such an extent that entire ecosystems are being eradicated and replaced or are being so modified or reduced in area that they can no longer maintain their previous diversity of living

organisms. This has meant a world-wide loss of genetic diversity, including the wholesale extinction of species, most of them small and of apparent little consequence to mankind. Only in a few obvious cases, such as some over-exploited whale populations or the apparent extinction of mammals such as the Thylacine and birds such as the Paradise Parrot, is public awareness alerted to the consequences of the extinction of species.

Ecologists and geneticists, however, have long warned of the consequences to human populations of any significant reduction in biotic diversity. Such consequences range from the loss of potential disease-curing drugs to population explosions of pest species when predators are reduced or eliminated. Loss of species may also have profound effects on human aesthetics; human "quality of life" is diminished by increased environmental homogeneity, to which lowered biotic diversity is a major contributor.

Economists have long argued that species and diversity have no intrinsic value and that alternatives are always available to replace extinct species or ecosystems. Others have argued that because extinction is the ultimate fate of every living species — some four billion species of plants and animals are believed to have lived on earth during about 3.5 billion years of evolution (Raup, 1986) — then extinction is a "natural" event and so should not be a cause for concern. There is, however, ample contemporary and historical evidence that if the rate of extinction increases, the changes to the earth's environments can be profound and that many of those changes will be deleterious to human populations.

The very first step in understanding the consequences of the changes which we are bringing about is to document the nature of those changes, including changes in the diversity, distribution and composition of animal and plant populations.

Basic to this process of documentation is the compilation of as complete an inventory as possible of the world's animal and plant species. Thus, taxonomy — the discovery and description of the kinds of animals and plants which inhabit our earth and their subsequent classification and naming — is not only an intrinsic quest for knowledge and a contributor to understanding of many processes in evolutionary biology, but is also an applied science basic to human welfare. Indeed, ecologists and other environmental scientists are seriously impeded in their work by lack of taxonomic knowledge of the animals and plants which they encounter, a barrier to understanding which French (1978) succinctly termed the "taxonomic impediment".

THE WORK OF THE TAXONOMIST

A taxonomist erects classifications using a variety of methodologies; some of these methodologies are discussed in a later Section. In all of these methodologies, however, the tools of the taxonomist's trade are attributes: some measurable or observable characteristics or functions of the individual organism. These attributes are analysed either by using a deductive, hypothesis-generating approach to identify those attributes (taxonomic characters) which most reliably infer relationships or by using algorithms (stepwise mathematical

procedures) which estimate coefficients of similarity and generate "family trees" or genealogical diagrams based on an analysis of shared features.

What kinds of attributes do taxonomists study? Traditionally, taxonomists have relied most heavily on structural features, external and internal morphology, to erect classifications. For example, birds are characterized by the possession (among many other characters) of feathers, mammals by the possession of hair or fur and reptiles by the possession of scales. All three of these groups are vertebrates which possess a backbone (vertebral column), in contrast to insects, spiders and worms (among others) which lack a backbone. This reliance on phenotypic characters (those observable structural and functional features which result from the interaction of the genotype with the environment) has inherent weaknesses in the reconstruction of evolutionary relationships, because such characters do not necessarily reflect either relationship or the degree of genetic divergence between different organisms.

With the development of appropriate techniques in cytogenetics and molecular biology, attributes of particular taxa which are direct expressions of genetic affinity can be identified. These expressions may be qualitative (for example immunodiffusion protein precipitation bands or the gross morphology of chromosomes) or quantitative (for example, the sequence of amino acids which make up particular proteins), but all have the advantage that they provide data which may be direct expressions of phylogenetic relationships and common ancestry. These techniques and their application to systematic and phylogenetic studies are described in greater detail by Baverstock (Chapter 12B), Baverstock & Schwander (1985), Ferguson (1980) and Wright (1974).

While the work of the taxonomist may be defined narrowly as the collection and analysis of data to produce a classification, in the real world a taxonomist must undertake a wide range of additional, sometimes routine, tasks before he or she can proceed with the basic process. These tasks may include: field work to observe or collect the animals which will provide the data for analysis; the preparation, preservation and labelling of those animals; the collection, preparation and care of specific tissues; or laboratory care of living animals.

Another important aspect of taxonomic research is a thorough knowledge of the published literature about any given group of organisms. This is important for two reasons. First, other researchers may have published information about particular animals (for example their morphology, behaviour, ecology) which will be useful to the taxonomist in erecting classifications. Second, a knowledge of the names which have been applied to taxa in the group being studied is essential if the taxonomist is then to apply the correct names to the taxa in his or her classification, or to avoid duplication. Fortunately, a number of nomenclators (lists of published names) is available to assist taxonomists (e.g. Neave, 1939–1940; Schulze & Kükenthal, 1926–1938; Sherborn, 1925–1932) while for many animal groups there are world-wide or regional nomenclatural checklists available (e.g. the *Zoological Catalogue of Australia*).

The nexus between classification (taxonomy) and names (nomenclature) will be emphasized later. The classificatory function involves three primary components: data collection, data analysis and the construction of classifications. Secondary components include such housekeeping tasks as the construction of keys and the preparation of formal descriptions.

The nomenclatural function involves the compilation of a complete list of names that have been applied to the animal(s) being studied and their name bearers; the examination of type specimens; the selection of new names, properly formed and treated, for undescribed taxa; the selection of

name-bearers for these new taxa and the careful adherence to other requirements of the international rules which govern zoological nomenclature.

These two functions come together in the preparation of the results of taxonomic research for publication. The format and presentation of taxonomic research papers tend to follow standard patterns, especially in the construction of diagnoses, descriptions, keys and synonymies, although editorial policy varies slightly from one scientific journal to another. Few journals specialize in taxonomic papers. Most taxonomic research is found scattered throughout a wide range of scientific journals. Such published research normally has been subjected to a peer-review system, but this varies widely in its rigour.

Mayr *et al.* (1953) and Blackwelder (1967) provide extensive discussions and guidelines for the conduct and interpretation of taxonomic research. Each of the major approaches to reconstructing phylogenies has inherent methodological strengths and weaknesses and the taxonomist's task is to select those methods which best suit a given taxonomic problem. There is no "right" way and slavish adherence to one methodology is a sterile approach to interpreting phylogenetic relationships. As Fitch (1984) has advised: "...take all absolutist pronouncements with a grain of salt, separate scientific utility from the ideological chaff, keep your options open, and enjoy the search for better ways".

Classification and the Origins and Development of Zoological Names

The functional objective of any classification is the efficient organization and grouping of things or concepts, or of information about those things or concepts, into categories which share common features. A classification is first and foremost a data storage and retrieval system, but a classification goes beyond the storage and retrieval of information. It also exploits correlation techniques to enable the user to predict the qualities or characteristics of a classified object which the user might never have seen or to predict from one set of observed qualities or characteristics other features of the same object which are unknown or hidden from view. An everyday example illustrates this point.

To say that one lives in a "home" tells another person little about the physical qualities of the place where one lives. The most universal definition of a home is that it is a shelter from the weather which is the fixed residence of one or more people. Depending on where one is in the world it may be a tent, a thatched hut, an igloo of ice, an apartment building, a cave, a mansion and so on. Indeed, about the only general physical quality we may predict from the classification "home" is that it will provide shelter from the elements.

A "house", on the other hand, provides much more specific predictable information. We may generally assume, without ever seeing it, that it will have a solid frame, a roof, external and internal walls, one or more rooms, beds, a kitchen or kitchen area and so on.

Similarly, merely by being told that a particular unseen animal is a bird, a zoologist would immediately know that the animal would, among other things, have feathers, be warm-blooded (homeothermic), lack external genitalia, have a high probability that it would have visible wings, could fly and that the female would probably make a nest, lay eggs, incubate them and provide parental care.

While classificatory systems may be independent of language (we rarely need to be told the sex of another person) concepts of classificatory groups are most effectively communicated by assigning names to them. There is, therefore, a clear nexus between classifications and the names which we

12A. CLASSIFICATION AND NOMENCLATURE

apply to the groupings which make up the classification. The study of the classification of animals (zoological taxonomy) inevitably embraces the study of animal names (zoological nomenclature).

Classifications may be "natural" or "artificial". Natural classifications are those which are based upon similarities and shared features derived from genealogical relationships. Classifying all animals which possess feathers into a single group — "birds" — is a natural classification because there is abundant evidence from fossil and living forms that all feathered animals share a common ancestry. Conversely, to classify into a single group called "fliers" all of those animals which possess wings and can fly, would create an artificial classification because there is equally abundant evidence that wings and flight have evolved many times in the course of the earth's history and that the ability to fly is not necessarily any indication of common genealogy.

In utilitarian terms, an artificial classification may be no less useful than a natural classification in data storage and retrieval. For example, a wildlife field guide might first ask the reader to categorize an observed animal by habitat, then perhaps by colour or behaviour and so on, gradually building up the following **hierarchical classification**:

- Found in rainforest
- Active by day (diurnal)
- Occupies the canopy
- Feeds on insects
- Black in colour

Clearly, such a classification says nothing about the genetic relationships of the animals in each of these categories, but it might quickly discriminate a particular animal observed in a rainforest.

The pre-Darwinian taxonomists realized that some animals were more closely related to each other than they were to other animals. The binomial classification developed by Carl Linnaeus in the 18th Century involved a clear expression of **perceived relationships**. In this sense it was, from the outset, a natural classification. With the development of evolutionary theory and genetics, this existing natural hierarchical system of zoological classification was found to contain all of the elements needed to express relationships through degrees of common ancestry. Such a system is termed a **phylogenetic classification**. The majority of zoologists today agree that the most valuable zoological classifications are those which most accurately reflect evolutionary relationships (phylogeny).

Whether a particular feature shared by two or more species is the result of common ancestry or merely an independent adaptation to a particular environment or lifestyle is often difficult to determine. For example, scaly skins are found in lizards, fishes, snakes, pangolins and crocodiles. Scales have evolved in each of these animals to protect the body in some fashion. Only when the embryonic development of the scales in each of these animals is studied and the possession of scales correlated with other shared characteristics, do we find that the scaly skins of lizards, snakes and crocodiles, while differing widely in appearance, is a character possessed by their most recent common ancestor. In this example, the scales of lizards, snakes and crocodiles are said to be **homologous**.

In fishes and pangolins, the scales develop embryologically in quite a different manner compared with those of lizards, snakes and crocodiles, or compared with each other. Moreover, the most recent common ancestor of each of these groups did not possess scales. We must conclude, therefore, that the scales of fishes and pangolins do not reflect genealogical relationships with each other or with lizards, snakes and crocodiles. For this reason the scales of lizards, fishes

and pangolins are not homologous, but are said to be **analogous** or **homoplastic** and each of these groups of animals independently has evolved scales as an adaptation to the need to protect the body. This is termed **convergent evolution**. To distinguish homologous (through descent) from homoplastic (through adaptation) characters is vital. Classifications erected on homoplastic characters are not phylogenetic.

Zoological Names

Before considering modern methods of zoological classification and the procedures adopted in applying formal names to the various categories in that classification, some understanding of the historical development of zoological names and categories is necessary.

Zoological names are universal, for they are used and understood by zoologists worldwide. Zoological names overcome language differences. For example, Australian and German zoologists would each recognize the zoological name *Trichoglossus haematodus*, although it is doubtful whether each would know it by the colloquial name applied by the other — Rainbow Lorikeet in English and Pinzelzungeng-Papagei in German! Even in the same language colloquial names can be misleading. Atlantic and Pacific Salmon are not, as might be expected from their names, either similar or related to the Australian Salmon. The latter is an advanced perciform bony fish of the family Arripidae, whereas Pacific and Atlantic Salmon are both primitive bony fishes of the family Salmonidae.

In basic form, the **zoological name** applied to any species of animal consists of two words, either or both of which may be arbitrary combinations of letters but which more often are Latin words or words from other languages that have been Latinized according to set rules. Thus, the zoological name of the Common House Mouse is *Mus musculus*, from the Latin word for mouse (*Mus*) and the Latin diminutive noun *musculus*, meaning "little mouse". The first of these two names represents the **genus** (termed the generic name) and begins with a capital letter while the second part of the name represents the **species** (the specific name) and always begins with a lower case letter. These (genus and species) and other categories in zoological classification will be explained in greater detail below, together with their basis in modern evolutionary biology.

The origin of this two-worded Latin zoological name (formally known as a **binomen**), however, predates the development of evolutionary theory by nearly a century. By the end of the 17th Century, many zoologists had begun to develop a "natural" classification of animals and to apply formal names to the categories in their classifications. There was, however, little consistency in the various approaches. Not until the publication of the Tenth Edition of his *Systema Naturae* in 1758 did the Swedish naturalist Carl Linnaeus (1707–1778) produce a work in which a binomial system of names was used throughout. The system proved so elegant and workable that it was quickly adopted by zoologists throughout Europe and has remained virtually unchanged to the present day. Indeed, so fundamental was the system developed by Linnaeus that the Tenth Edition of the *Systema Naturae* has been universally accepted as the formal beginning of zoological nomenclature and names proposed before that publication, even if in binomial form, are not legitimate unless expressly validated by use after 1758.

What were the advantages of such a system over earlier ones? First, it provided a universal or international name which was independent of local languages or dialects. The power and universality of such a system are shown dramatically in Fig. 12A.1, in which extracts from scientific research papers from around the world have been brought together.

Few biologists would be able to read all of the languages shown in Fig. 12A.1, but nearly all would know at a glance that each paper dealt with some aspect of the biology of the Common House Mouse!

Second, the binominal system provided an effective data retrieval system in which each part of the binomen represented a distinctive set of morphological and ecological data and which allowed new species (*i.e.* new data sets) to be slotted into the existing classification in a systematic fashion. These advantages have been retained to the present. Alternatives to the Linnaean system of classification are discussed by Wiley (1981).

While the Latin binomen has proved its worth for more than 200 years, the biological concepts which are expressed by the two parts of the binomen have changed dramatically since Linnaeus' day. At that time, the biblical account of Genesis was accepted in its literal sense by most naturalists. By this account, all kinds (species) of animals were created at the same point in time and species were immutable. While the discovery of fossil animals which are not represented on the earth by extant forms convinced all but the most bigoted observers that extinctions had occurred, these were again attributed to a single catastrophic event: the biblical flood.

With the development of the geological and palaeontological sciences in the early 19th Century and the growing fossil and biological evidence for the transmutation of species in time, a growing body of scientists was accumulating the data which would lead Charles Darwin and Alfred Russel Wallace to develop and refine a theory of the evolution of animals and plants by natural selection. While their original theories were developed without any understanding of the genetic basis of evolution, they laid the foundation on which modern evolutionary science has been built. To Charles Darwin and his contemporaries, a knowledge and understanding of the classification of animals and plants were critical precursors to the development of their evolutionary theories.

Zoological Classification

Zoological classification is hierarchical. By this term is meant that each level of the classification embraces all of the features characteristic of the levels below it. We can best illustrate this by example. Figure 12A.2 shows the major categories used in an hierarchical zoological classification and the levels and categories whose names are governed by the *International Code of Zoological Nomenclature*. In Fig. 12A.3 is shown the classification of the house mouse in such a system and some of the features which characterize each classification level of the house mouse. From this classification, any zoologist could build up quite a complete picture of a house mouse. The features which characterize each level of the classification include not only those which define that level but also each of its higher levels.

In the example shown, just a few of the characteristics which define each level have been selected in order to demonstrate the way in which an hierarchical classification can be used to build up a data set about any particular member of the hierarchy. A corollary of such a system is that anyone with knowledge of the classification would know, if handed an animal with the name *Mus spretus*, that it would share with the common house mouse all of the characteristics of the genus *Mus* and of its higher categories.

While the information content of such a classification can be formidable, the system also has considerable predictive power. For example, a newly discovered animal can be diagnosed quickly and slotted into an existing classification on the basis of a small suite of highly correlated characters. Having done

so, the probability is very high that it will possess all or most of the other characteristics which have been used to define the higher levels of the classification.

The categories in the hierarchical classification shown in Fig. 12A.2 fall into two distinct groups: those at the species level and below (species, subspecies) and those higher categories which represent groups of species (such as genus, family, class). Those at the species level are widely (though not universally) accepted to represent objective categories; they have the potential to be defined in quantifiable and ultimately testable genetic terms. Higher categories, on the other hand, are by definition subjective; groupings of species must always require an arbitrary decision about the boundaries of the group.

What is a species? This is one of the most difficult and intractable questions in modern biology. While definitions abound, so do exceptions to those definitions. The conventional and most useful definition of a species is that of Mayr (1940): "species are groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups". It follows that the offspring resulting from any interbreeding between species must be infertile.

While this definition has been reworked by later biologists, the changes have been in terminology rather than in meaning. Species comprise groups of individuals, each with its own unique complement of genetic material, but each with the potential to exchange some of that material (that is, to interbreed) with other members of the same species. In other words, species represent unique and independent gene pools which must be able to maintain their uniqueness in the face of competition from other species. This interpretation of a "species" is known as the **biological species concept**, whereby species are not only objectively defined, but represent the basic or fundamental evolutionary unit in nature.

Unfortunately, there are difficulties with this definition when it comes to species which reproduce asexually or when species interbreed under artificial conditions to produce fertile offspring. For this latter reason, the definition is confined to "natural populations".

In practice, most species-level taxa are defined on probability rather than on unequivocal genetic criteria. And, for evolutionary biologists as well as taxonomists, the process that gives rise to species — the speciation process — is at the very heart of evolutionary and systematic biology.

SPECIATION, PHYLOGENY AND PHYLOGENETIC RECONSTRUCTION

Speciation

As outlined above the **biological species concept** is one which regards the species as the largest of the basic reproductive units in nature. As such it is a fundamental evolutionary unit which has the potential to be objectively studied and defined. There have been many criticisms of this concept, principally from those biologists with a strong background in mathematics and logic.

While the biological species concept has some metempirical qualities, there can be little doubt that the concept provides the best means of identifying those patterns of speciation and biological genealogy against which to test hypotheses about evolutionary processes.

The **evolutionary species concept** developed by Wiley (1978; 1981) has a number of functional advantages over the biological species concept. An evolutionary species consists of

小家鼠 (*Mus musculus* Linnaeus) 野外种群生态的研究, 在北方有青海省生物研究所新疆鼠害研究组(1975)的新疆小家鼠数量季节性变化的研究, 而在华南地区, 这类系统的研究尚不多见。本文仅涉及珠江三角洲农田小家鼠的食性、繁殖和寄生线虫等方面, 并对

EIN SUBFOSSILES VORKOMMEN DER HAUSMAUS (MUS MUSCULUS (s. l.) AUF MADEIRA)

Von Harald Pieper *

R e s u m o . Em Setembro de 1979 o autor encontrou na península de São Lourenço no extremo leste da Ilha da Madeira restos subfósseis de *Mus musculus* (s.l.). Em duas visitas posteriores mais material foi encontrado. As medidas dos ossos são consideravelmente maiores do que as de *M. m. brevirostris* e lembram o material subfóssil da Península Ibérica. Apesar de não ter esclarecido inteiramente a idade, o achado de qualquer maneira é importante visto que é um dos exemplos raros da existência de mamíferos terrestres não voadores em ilhas «oceânicas» longe de

sóes maiores, provavelme

ressant d'analyser quelques souris et mulots provenant d'Iran. Les données les plus généralement admises sur la faune de ce pays font état d'une seule espèce de *Mus* et d'*Apodemus*, les souris étant attribuées à plusieurs sous-espèces de *Mus musculus* et les mulots désignés sous le nom d'*Apodemus sylvaticus*

Un approccio sistem
gici aveva comportato un
linneana *Mus musculus*
ficavano notevoli confus
specie (cfr. RODE, 1947).
veduto ad una complet
musculus e ZIMMERMANN
nistico. NIETHAMMER
della dinamica zoogeografica delle diverse sottospecie europee e mediter-

اجريت الدراسة في أحد حقول الجب في أبي غريب للفتررة من
أيلول 1983 وإلى آب 1984 . لقد وجد بأن الانواع المتواجدة من
القوارض في العقل هي :

فأر البيت *Mus musculus* L. والجرذ الهندي البانديك _____ و
نوسوكيا *Nesokia indica* Gray & Hard.
(الطرطورة الهندية) *Tatera indica* Hard. . لوحظ من الدراسة
 بأن هناك عذيب مستمر في نسبة تواجد فأر البيت مرتفع
 بارتفاع نسبة تواجد أحد النوعين المباقيين أو كلاهما . كما

tavují dosud významný ekonomický obuží konzumací a znehodnocováním jednotlivé druhy i na přenosu a at, ale i lidí (zoonózy). K budovám lmi populacemi myši domácí (*Mus musculus*) a biotopů stahuje další h farem vytvářejí specifická spole- avně v podzimním období, na jate do volné přírody. Výzkum proble- zavřen (Kučeruk 1946, Zimina k a Porkert 1973, Beljajev a l. 1978). Poměrně málo je dosud jících velkokapacitní objekty živo-

МЕХАНИЗМЫ АВТОРЕГУЛЯЦИИ ПЛОТНОСТИ В ГРУППИРОВКАХ ДОМОВОЙ МЫШИ (*MUS MUSCULUS*) С РАЗЛИЧНЫМИ ТИПАМИ ПРОСТРАНСТВЕННОГО ПАСПРЕДЕЛЕНИЯ

Gattung

Hausmäuse - *Mus* L.

Hausmaus - *Mus musculus* L.

Kennzeichen: Muffiger Mäusegeruch! ♀ sind größer u. schwerer als ♂. - V. Im Anschluß an den Menschen fast kosm verbreitet, von Island bis in die Trop. Wildformen in pal Steppen von N-Afr bis O-As. Stammform der Laboratoriumsmäuse.

Hausmaus - *Mus musculus domesticus* RUTTY (Abb. 323/1)
G. Os braungrau, Us heller grau, ohne Trennungslinie. Im NW schwärzlich gefärbte Sippen. Schw meist länger als K + R. K Schw 82-90, Ohr 12,5-14, Hf 15-20, CB 19,3-23,0 mm

house mouse, *Mus musculus*, to exploit opportune plagues in the cereal belts of south-eastern Australia lagues often cause large economic losses and high ities (Ryan and Jones 1972; Saunders and Robards lly low in the years between plagues, when mice are



En la presente nota se expone las rectas de regresión calculadas entre el peso y la longitud de la mandíbula y la longitud total del húmero, fémur y coxal de *Mus musculus* comensal del Nordeste ibérico y se comenta su aplicación al estudio de la alimentación de las estrigidas. La longitud de la mandíbula se considera oportuno utilizarla para aquellos casos en los que se desconoce a qué especie pertenecen los restos de esqueleto postcraneal.

Figure 12A.1 Zoological names represent an international language through which zoologists can communicate the identity of animals studied. In the extracts from scientific papers shown the reader can immediately recognize the species used in the various studies: the cosmopolitan house mouse, *Mus musculus*.

[mouse by M. Robinson]

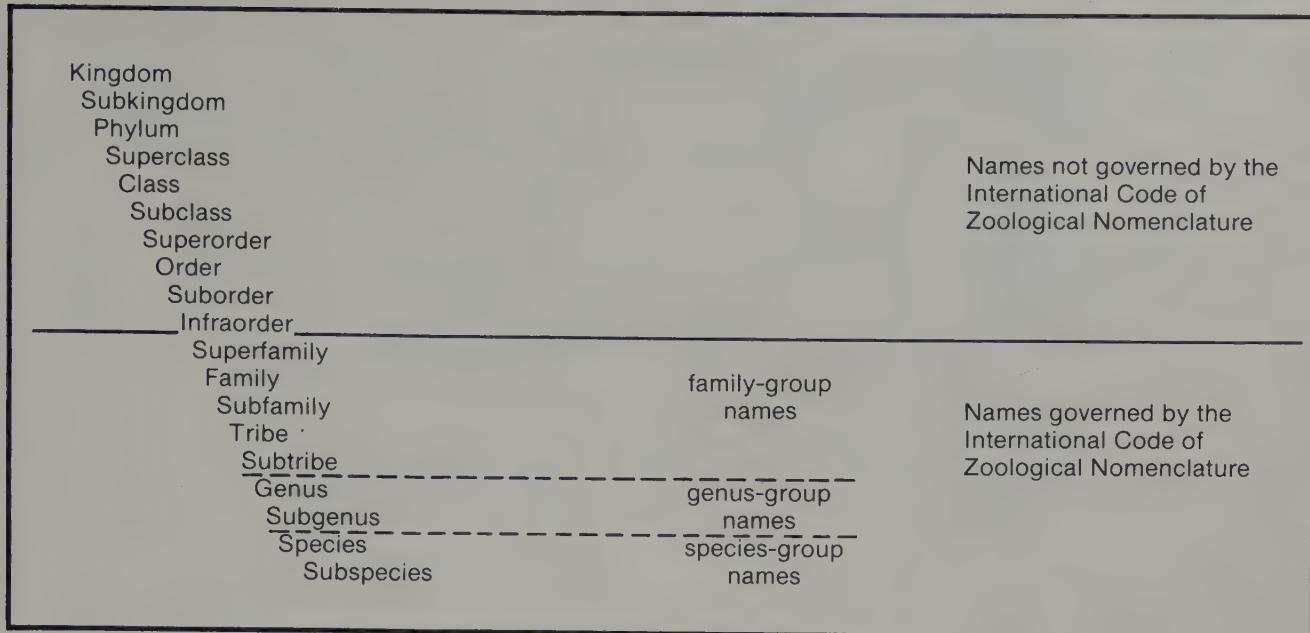


Figure 12A.2 The major categories in the hierarchical classification of animals. Only the names of superfamilies and lower, or subordinate, categories are governed by the *International Code of Zoological Nomenclature*. While the names of higher categories are usually subject to widely accepted convention, they are not governed by the *Code*.

a lineage of one or more **demes** (or, rarely, asexually reproducing populations) bound by common ancestry and an ability to maintain its integrity as a species from those lineages representing other evolutionary species. A **deme** is a local group of randomly interbreeding individuals. In treating a species as a lineage through time, this concept more closely reflects the evolutionary process.

Depending on a variety of intrinsic (*e.g.* mutations) and extrinsic (*e.g.* geographic separation of the demes) factors, the opportunity for individuals to disperse between demes and so exchange genes, will vary widely. **Speciation** is the process whereby one or more demes become isolated reproductively from other demes (or asexual populations) of their evolutionary species and by this isolation acquire the potential to found a new species.

An idea long held as an axiom was that for a deme to become isolated from its parental deme(s) there must be some effective barrier, extended in time, to prevent its members from dispersing to other demes and *vice versa*. Such isolation could occur only as the result of the geographic isolation of one deme or group of demes from others, a process known as allopatric speciation. Allopatric speciation is now known to be only one (albeit the most important) of several potential speciation mechanisms which may be invoked to account for the origin of species. The basic mechanisms may be summarized as follows:

Allopatric speciation involves the total isolation of one or more demes of a species from their sister demes by barriers which prevent the interchange of individuals between the two groups. While such barriers may be physical (such as mountain ranges or oceans) or ecological (such as intervening areas of unsuitable habitat), each barrier must represent some level of spatial (geographic) separation and isolation. The allopatric speciation model requires that isolation be continuous for as long as it takes for the isolated populations to develop reproductive isolating mechanisms or to establish reproductive incompatibility, so that if the barrier is removed

then the populations can again come together without hybridizing. The essential features of allopatric speciation are shown in Fig. 12A.4a.

Sympatric speciation is a process whereby individuals within a single deme or population are able to develop characteristics of morphology, behaviour, habitat preference, *etc.* which lead to successful mating only with those members of the same deme or population which share the same characteristics. This process of selective mating ultimately leads to the development of fixed genetic differences which prevent gene flow between the two subgroups.

While presumed examples of sympatric speciation have been cited occasionally, there is wide agreement that sympatric speciation (as distinct from stasipatric speciation, see below) is theoretically impossible in bisexual species. It might well be an important mechanism, however, in certain parasitic or parthenogenetic organisms (Bush, 1975). Many examples of apparent sympatric speciation are attributable to allopatric or parapatric speciation of "demes within demes", a process for which the term "quasi-sympatric speciation" has been coined by Pielou (1978) and which is illustrated in Fig. 12A.4b.

Parapatric speciation at first sight appears to be intermediate between allopatric and sympatric speciation. It describes a situation in which adjacent and (at least partly) contiguous demes or populations become reproductively isolated from each other, despite the apparent opportunity via their adjoining boundaries for the exchange of individuals and their genes (Fig. 12A.4c). In this case, however, the adjacent demes or populations are able to develop and maintain fixed genetic differences, despite the interchange of individuals, because such differences offer selective advantages in each of the areas occupied. As Pielou (1979) has pointed out, the difference between allopatric and parapatric speciation is not merely one of the size of the gap between populations, but involves a fundamental distinction: "...in allopatric speciation, the separated demes ultimately develop reproductive isolation because there is no gene flow between

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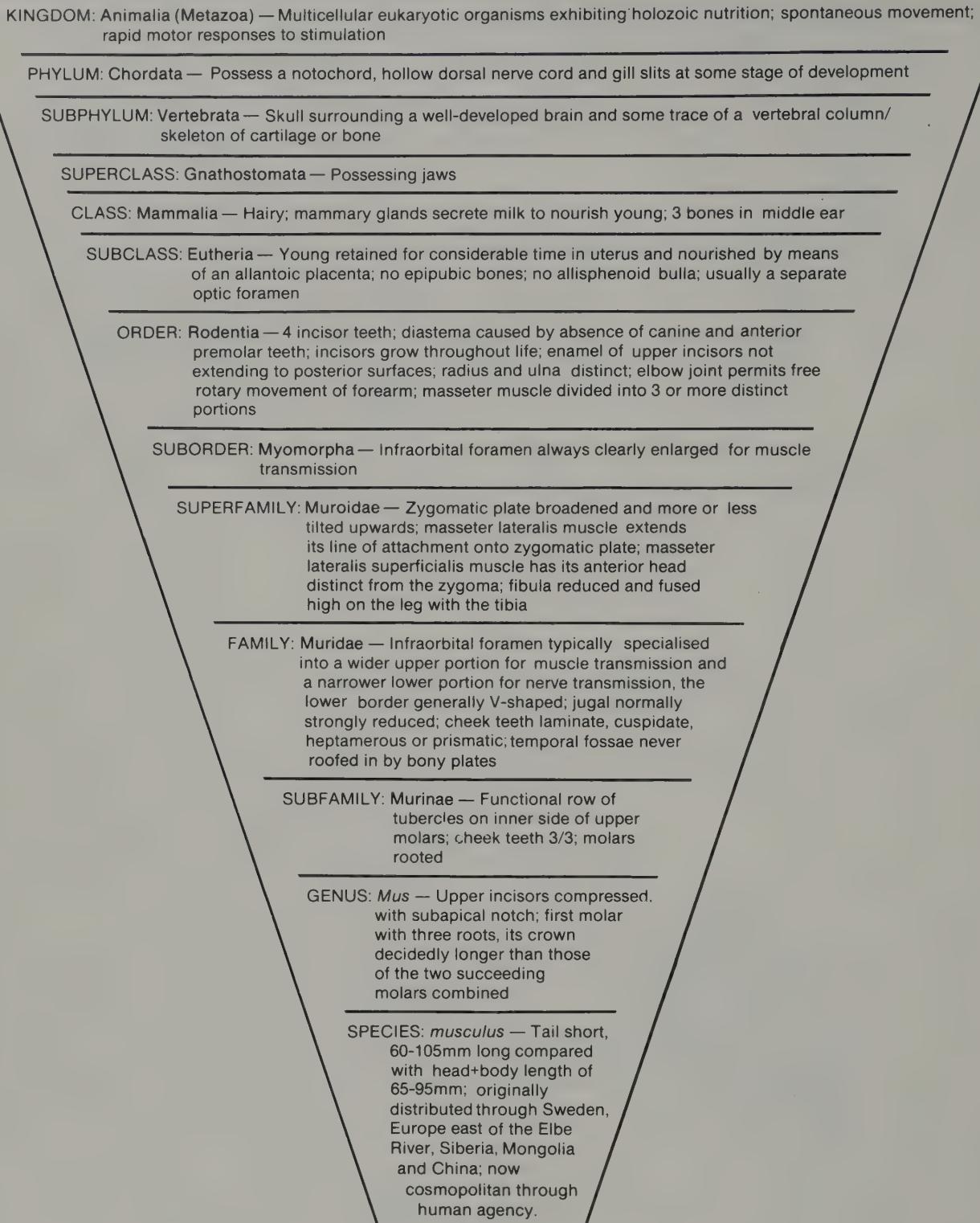


Figure 12A.3 This figure demonstrates the data storage and retrieval capacity of an hierarchical zoological classification. The features which characterize a taxon at any level are common to all of its lower (subordinate) taxa. Thus a very full description of a taxon at any level can be obtained by adding to the features which characterize that level plus those that characterize all of the higher levels of its classification. In the example shown a description of the house mouse, *Mus musculus*, comprises all of the features which make up the classification contained in the inverted pyramid.

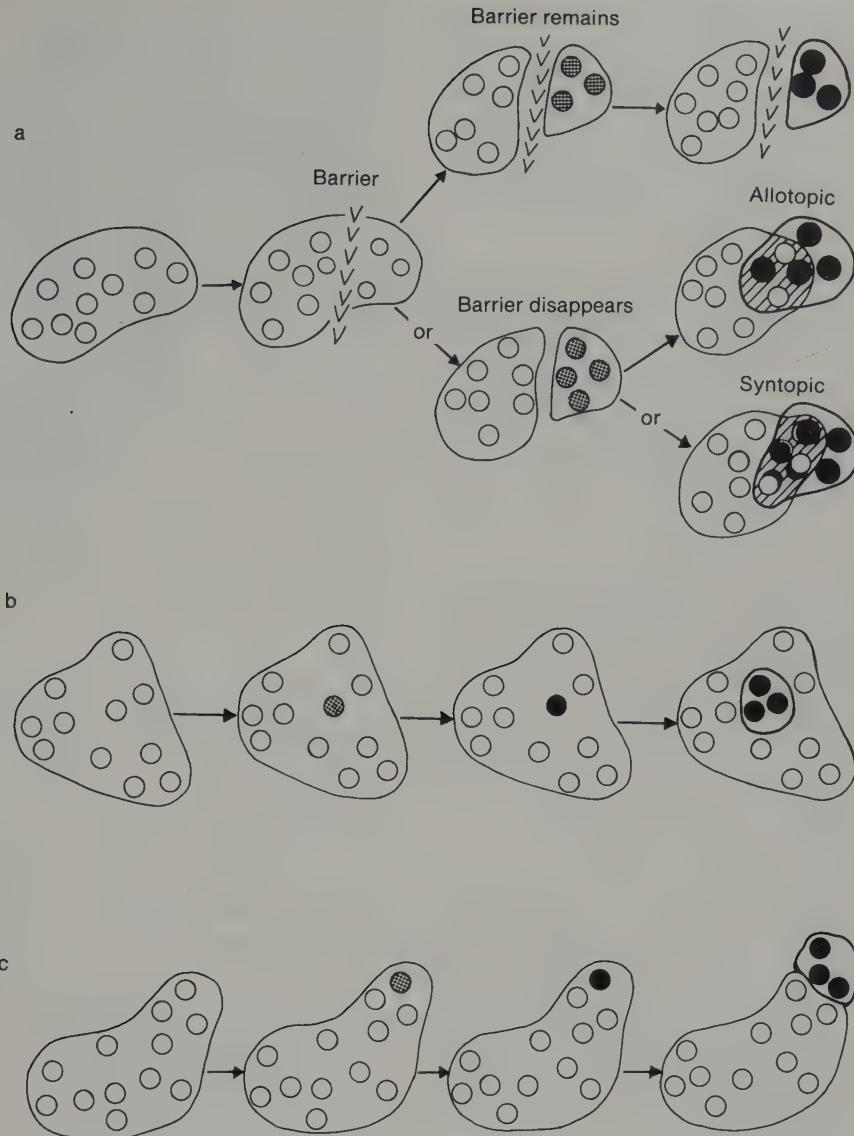


Figure 12A.4 Some models of the process of speciation. a. Allopatric speciation. Here an originally continuous population is split into two by a physical or other barrier, effectively preventing genetic exchange between the two groups. Over time, genetic divergence occurs between these groups such that successful interbreeding cannot occur if the barrier is removed. The two species may then occupy a common geographical area either in the same (syntopic) or different (allotopic) habitats. b. Stasipatric and quasi-sympatric speciation. Here one or more demes within the range of a species develop fixed genetic differences from the remainder of the population, either by natural selection due to localised isolation effects (quasi-sympatric speciation) or by chance fixation of chromosomal mutations (stasipatric speciation). c. Parapatric speciation. Here one or more peripheral demes develop fixed genetic differences from the remainder of the population. Two species result whose ranges are contiguous but do not overlap. O deme of parent species A; O deme of species A in which genetic differences have developed which are insufficient to prevent successful interbreeding with members of other demes; O deme of daughter species B in which genetic differences between it and demes of its parent species A have become fixed and so prevent the exchange of genetic material (interbreeding) between demes of the two species. Limits of species A shown as a thin line; limits of species B shown as thick line.

them. In parapatric speciation, the demes develop reproductive isolation in spite of a certain amount of gene flow between them".

Considered by some to be a special case of parapatric speciation (White, 1978) and by others to be a form of allopatric speciation (Wiley, 1981), stasipatric speciation involves the production in a particular deme, by mutation, of a chromosomal rearrangement which, in its homozygous condition, is not only viable but infers a selective advantage over those members of the deme possessing the heterozygous condition. Consequently, by genetic drift or perhaps by inbreeding, the mutant condition becomes fixed and thus gives rise to a new species. Such mutations are random and, while

dependent on a whole suite of environmental conditions for their fixation, give rise to stasipatric speciation in random geographic fashion.

The Darwinian theory of evolution by natural selection sought to explain all evolution in terms of the gradual accumulation of small adaptive changes, a view which was given a new basis in genetics by Dobzhansky (1935; 1937) and Huxley (1942). This new, synthetic view of evolution retained the basic Darwinian model, but supplemented it by modern knowledge of genetics, molecular biology and palaeontology and so led to the establishment of what was termed the neo-Darwinian school of evolutionary theory. The status of this theory and its methodological strengths and weaknesses are explored fully by Riddiford & Penny (1984).

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One of the problems which confront biologists in the application of Darwinian gradualism as the sole explanation of the evolutionary process is the evidence in the fossil record that long periods (in geological terms) of relative stability (stasis) were broken by relatively brief periods in which major changes occurred in entire world faunas. Whole groups or subgroups of organisms might suddenly disappear from the fossil record, while other groups may experience explosive radiations in which they rapidly diversify.

Many attempts have been made to explain these large or macro-evolutionary changes and the sudden rapid changes from one form to another ("saltations") which punctuate the fossil record. Some (*e.g.* Kemp, 1986) regard the problem as, at least in part, an artefact of the limited resolving powers of palaeontology. Others (*e.g.* Raup, 1986) have identified a periodicity in mass extinction events throughout earth history. These events have been attributed to comet impact events, but could be attributed as readily to other cyclical phenomena in the solar system.

Eldredge & Gould (1972) believe that the fossil evidence is so compelling that they propose a supplementary theory of "punctuated equilibria" to explain the fossil record. This theory states that adaptations are not always slow and cumulative as the Darwinian evolutionary model predicts but, once acquired, may be remarkably stable over time. They postulate that such stability is periodically interrupted by short (in geological terms) spurts of morphological (and genetic) change. Eldredge & Gould observe that adaptations, rather than bringing about continuous change in species over time, appear to be remarkably stable over the course of their existence in any given species.

Many zoologists regarded the "punctuated equilibrium" model as an attack on Darwinian gradualism and the traditional mechanisms that have been proposed to explain the speciation process. As Eldredge (1986) points out, however, punctuated equilibria seek to explain yet another observation in the fossil record: that newly evolved (descendant) organisms do not necessarily replace the organisms from which they are derived (ancestors), but that both groups often continue to live side by side for long geological periods.

Eldredge & Gould (1972) did not abandon the allopatric speciation model of evolution nor did they abandon the Darwinian model of microevolution leading via adaptation to macroevolutionary changes. They have proposed, however, a major change in the Darwinian concept of the continuous transformation of species via minor adaptive changes to one in which species are fixed entities, each with its own birth, longevity and death. Thus, periods of rapid evolutionary change in the fossil record represent the interaction of large-scale economic (*e.g.* ecological) and genealogical systems (Eldredge, 1986). This last aspect of the punctuated equilibrium theory seemingly is most in conflict with neo-Darwinian evolutionary theory because it calls for some additional mechanism, operating at a higher level than the deme, to explain observable macroevolutionary phenomena.

Phylogenetics and Phylogenetic Reconstruction

The animal species which currently inhabit the earth are the products of more than 3.5 billion years of successive cycles of speciation and extinction and so retain in their physical and genetic constitutions many clues as to their relationships with earlier life forms. **Phylogenetics** is the study of such relationships. The objective of phylogenetics is to reconstruct the evolutionary history of living and extinct species.

Systematic zoologists (of which taxonomists are a subset) are thus concerned with the classification of animals in a way which best expresses the phylogenetic relationships of the animals being studied. Three distinct, but overlapping, methodologies currently are used to establish biological classifications which reflect phylogeny. Their major proponents have tended to regard these methods as mutually exclusive, but each has advantages and disadvantages which call for selective use of those aspects of all three methodologies which best address particular taxonomic problems. Unfortunately, a plethora of different and often confusing names has been applied to these methodologies by their opponents and proponents and these are listed below.

No matter which methodology is adopted by the taxonomist, however, the objective is usually twofold: to produce a classification and, depending on the method used, to express either relationships (genealogy) or levels of similarity between the groups produced in the classification. Traditionally, these last objectives are expressed through branching diagrams in which the lengths of the branches represent time or coefficients of similarity, the relative thickness may represent relative diversity, the branching points represent speciation or other evolutionary events. Some examples are shown in Fig. 12A.5.

Before examining each of the methodologies mentioned above, however, some of the common terms and concepts involved in the various kinds of phylogenetic analysis must be considered briefly.

The evolution of one species from another by one of the speciation mechanisms described above it is known as a **speciation event**. **Phylogenetic reconstruction** is, therefore, an attempt to document the sequence of speciation events leading to the evolution of particular species or groups of species representing higher taxonomic categories.

When all of the taxa represented in a particular phylogenetic series not only can be derived from a common ancestor, but also include all of the known descendants of that common ancestor, then the series is said to be **monophyletic**. For example, a series containing only marsupials would be a monophyletic series. Conversely, if the taxa in the series cannot be derived from a common ancestor or the most recent common ancestor is not itself a member of the series, the series of taxa is said to be **polyphyletic**. Thus, a series containing only pangolins and crocodiles (see earlier discussion) would be regarded as a polyphyletic group.

Where all of the taxa in a phylogenetic series can be derived from a common ancestor, but the series does not include all of the known descendants of that common ancestor, then the series is termed **paraphyletic**. Farris (1974) demonstrates, for example, that the Class Reptilia, by excluding groups (such as birds) which are descended from reptiles, is a paraphyletic group.

Individual animals or taxa may be described by a series of **characters**; these are observable attributes which may be morphological, behavioural, physiological, biochemical, genetic, etc. Such characters vary in their exact expression in different individuals and different taxa. Such variations are known as different **character states**.

Thus, in a study of higher vertebrates the wings of birds and the flippers of dolphins represent different character states of the character "pentadactyl limb". At a lower taxonomic level, such as a study of birds, the wing may be treated as a character and its relative size in different species treated as different character states.

Homologous characters, as indicated previously, are those characters shared by different taxa and which existed in their common ancestor (shared homologues). Homologous char-

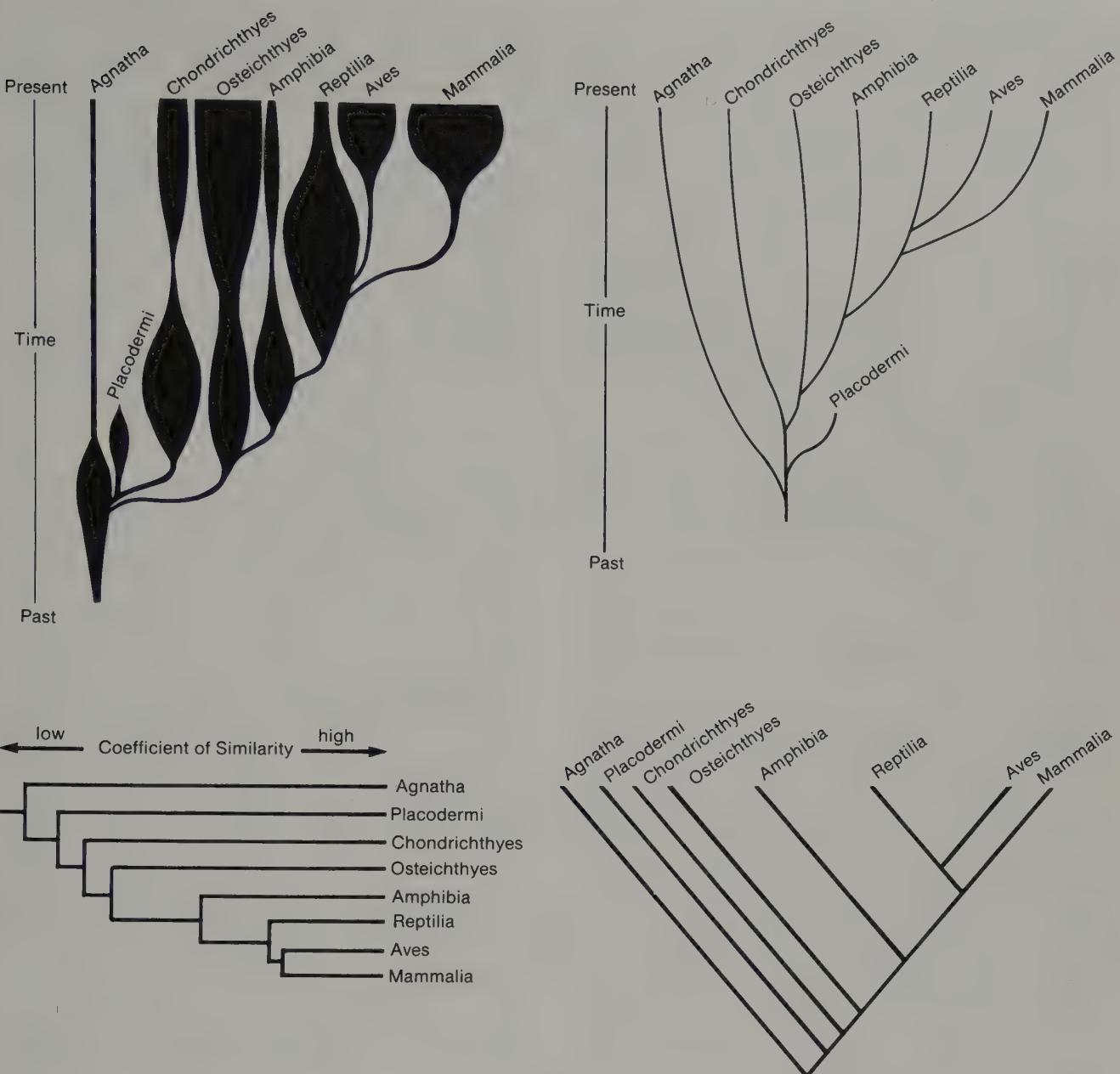


Figure 12A.5 Symbolic representations of zoological classifications. a. An evolutionary tree of the major groups of vertebrates. In this tree time is represented by the vertical axis while the relative diversity of each group (number of species) at any point in time is represented by the relative width of the branch. b. The same tree more simply expressed as a bare branched tree with relative diversity omitted. c. A phenogram of the same groups of vertebrates based on a statistical comparison of the proportion of features shared by each pair of groups; thus the horizontal scale represents a statistical measure of similarity. d. A cladogram of the same groups in which the common ancestor of each pair of groups is represented by the branching point at which the two groups separated. The degree of relationship between groups is represented by the lengths of the branches which separate them.

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acters also may be any pair of characters in a phylogenetic sequence or lineage in which one character is derived from the other.

Just as species change and evolve, so too do characters, often independently of the speciation process. Changes in homologous characters over time, however, mean that for every pair of different but homologous characters, one must have appeared prior to the other. The earlier of these two characters or character states (the first to appear) is known as the **primitive, generalized or plesiomorphic** condition, while the later character or character state (the second to appear) is known as the **advanced, derived or apomorphic** condition. These two conditions are known as the **phylogenetic polarity** of the characters or character states being considered and apply only to that particular comparison. It follows that a character or character state which is plesiomorphic in one lineage may be apomorphic in another.

Where homologous characters shared between two taxa originated in an evolutionary lineage before the appearance of their most recent common ancestor, the homologue is termed a **symplesiomorphy**. If, on the other hand, the homologous characters are traceable only as far back as their most recent common ancestor, the homologue is termed a **synapomorphy**.

In any given sequence of speciation events linked by common ancestry, the species which make up this monophyletic lineage can be grouped into higher (supraspecific) taxa known as **clades**.

Returning to the construction of phylogenetic zoological classifications, the three competing methodologies, to which reference was made above, may be described briefly as follows:

EVOLUTIONARY SYSTEMATICS (also known as evolutionary classification, morphological systematics, phenetics and phenetic systematics) is a logical development of "traditional" or "orthodox" systematics which had its origin in the Darwinian method of inferring evolutionary history from observed differences and similarities. In original form, it involved the intuitive weighting of characters or attributes based on knowledge (experience) of variation in particular groups of organisms. Darwinian systematics still is practised widely by taxonomists today, often under the guise of modern methodologies and their specialist terminologies.

In the modern, most rigorous form, evolutionary systematics utilizes as many characters (attributes) as possible, including those of anatomy, ecology, genetics, biochemistry and behaviour. It relies heavily on correlation techniques to identify suites of characters which indicate patterns of common ancestry and to draw up genealogical trees (phylogenograms) which identify the sequence and extent of divergence (location and length of the branches) of the component taxa in monophyletic or paraphyletic assemblages of taxa. As pointed out by Mayr (1981), the "presumed relationships have to be tested again and again with the help of new characters, and the new evidence frequently leads to a revision of the inferences on relationship." Evolutionary systematics also infers that small, cumulative changes in a "species" over time can lead to the gradual evolution of new species without the need to invoke a particular speciation event in which two "daughter" (*i.e.* "sister") species arise from a "parent" species. Conversely, as a result of several concurrent vicariance events isolating several demes of the same species, more than one new species in a lineage can evolve concurrently. A **vicariance** event occurs when a natural barrier is formed which divides a previously continuous biota into isolated parts.

PHYLOGENETIC SYSTEMATICS (also known as phylogenetics, cladistic systematics and cladistics) derives primarily from the work of Hennig (1950), in which all phylog-

eny can be expressed as a series of individual speciation events in which two daughter (sister) species evolve from a common parent species which itself ceases to exist from the time that the two daughter species come into existence. Cladistics is concerned with the identification of monophyletic groups and some cladists reject the paraphyletic groups of evolutionary systematists as "artifacts" (Patterson, 1982). Such a stance, however, fails to recognize the distinction between phylogeny and the subjective and functional classifications which might be derived from particular phylogenies.

Despite the attempts of some cladists to justify polychotomies (see Felsenstein, 1978), there follows from the cladistic thesis that all genealogical trees (cladograms) derived from phylogenetic systematics must show only dichotomous branching. Each branching point links pairs of sister groups to their hypothetical parent species and its origin is that hypothetical species (the stem species) which is a common ancestor only to the real species which lie at the tips of the terminal branches of the cladogram.

An excellent summary of the principles and practice of phylogenetic systematics is provided by Janvier (1984). The analytical methods of phylogenetic systematics are in theory much more objective and quantitative than those of evolutionary systematics; they are explained fully in Wiley (1981). There can be difficulties, however, in their application and practice.

First, the method is dependent on the accurate identification of monophyletic lineages, itself dependent on the accurate identification of homologous characters. Consequently, the use of non-homologous (homoplastic) convergent characters leads inevitably to spurious phylogenies. Strauch (1984) has proposed, however, a character compatibility method for identifying and utilizing phylogenetically reliable information in homoplastic characters so that they can contribute to part of an overall cladogram.

While homologous characters can be identified fairly reliably among higher taxa, especially in those groups (such as vertebrates) which are well known morphologically and taxonomically, reliability decreases at lower taxonomic levels, especially in poorly studied groups.

Cladistic analysis, if it is to accurately reflect phylogeny, is also dependent on the accurate identification of the phylogenetic polarity of the homologous characters selected for the analysis. Three principal methods have been proposed. The major method for testing whether a particular character state or one of a pair of homologous characters is plesiomorphic or apomorphic is that of **out-group comparison**: the condition of the character (or character state) in one monophyletic group is compared with that in its sister group (out-group). If one character or character state is found only in the monophyletic group while the other is found in both the monophyletic group and its sister group, then the character shared by both groups is the plesiomorphic (primitive) character while that confined to the monophyletic group will be the apomorphic (advanced) character. Remember that in the dichotomous cladogram only one true sister group can exist, so that the selection of the wrong out-group will result in the identification of spurious synapomorphies and symplesiomorphies. This is not a criticism of the cladistic method but of its practical application.

Only apomorphic characters can be used to identify the branching points in a cladogram. Plesiomorphic characters have little or no value in reconstructing phylogenies in phylogenetic systematics.

The other major method for determining the phylogenetic polarity of characters has been termed the "ontogenetic method" (Nelson, 1978) or "pattern cladistics" (Beatty, 1982).

Ontogeny is the history or pattern of development and growth of an individual organism throughout its life. During this process of development and growth particular characteristics are "transformed": for example, the chewing mouthparts of caterpillars are transformed to the sucking mouthparts of the adult.

As a method for determining the phylogenetic polarity of such characters, the ontogenetic method assumes that when characters are transformed during ontogeny "...from a character observed to be more general to a character observed to be less general, the more general character is primitive and the less general advanced" (Nelson, 1978).

A particularly enlightening discussion of the ontogenetic method and its relation to other methods for determining phylogenetic polarity of characters, is provided by de Queiroz (1985).

The third method for determining the phylogenetic polarity of characters is termed the "palaeontological method" and can apply only to those homologous characters observable in fossils. This method assumes simply that in any comparison of such homologous characters then the one which is found in the earliest (*i.e.* oldest) fossil must, *ipso facto*, be the primitive or ancestral condition and the one found in later fossils derived.

Two principal analytical techniques are used in cladistics. The first seeks to achieve the most "parsimonious" cladogram, that is, the one which best fits the data and which requires the minimum number of *a priori* assumptions to explain the data. Consequently the most parsimonious cladogram will be the shortest that can be derived from the available data.

The second method seeks to achieve maximum "compatibility" with the available data by finding the largest number of characters compatible with a particular phylogeny without concern for the number of character state changes needed to account for the characters used.

Both methods, of which there is a number of variants, require the application of sophisticated statistical techniques and these are discussed by Felsenstein (1984).

There has been much discussion generated in recent years (*e.g.* Hull, 1984; Janvier, 1984) on the "transformation" of cladism from Hennig's original concept of an analytical method based on the speciation process to that of the identification of hierarchical patterns of "nested characters", whether or not such patterns reflect speciation events (Platnick, 1979).

A major problem in cladistics (although certainly not confined to this method of phylogenetic analysis) is that in examining possible relationships among a given group of taxa the number of theoretically possible cladistic patterns is vast, even when dealing with only a handful of taxa. With large numbers of taxa, the potential relationships are almost infinitely large and so each error in assigning phylogenetic polarity or in identifying monophyletic lineages can compound the probability of producing a spurious phylogeny. This problem is emphasized by Baverstock (Chapter 12B).

NUMERICAL PHENETICS (also known as phenetics and numerical taxonomy), unlike the previous two methodologies, makes no attempt to identify and select for analysis those characters or attributes which have greater phylogenetic information content than others. Rather, all characters are given equal weight or value in the initial analysis. As many characters as possible are used and are assigned numerical values to provide a measure of overall similarity. These data sets are then analysed using a variety of algorithms to produce a tree (phenogram) which, in statistical terms, represents the most parsimonious expression of the similarities between the characters analysed. This phenogram may then

be used as the basis of a classification, with the distances between branching points (phenetic distances) equated with the hierarchical levels of a zoological classification.

In practice, most numerical phenetists work with taxonomic units which they equate with some level of a phylogenetic hierarchical classification — usually the species. Whereas phylogeneticists regard the species as a fundamental taxonomic unit, numerical phenetists treat the species as only one of a number of operational taxonomic units (OTU's).

The major advantage of numerical phenetics claimed by its proponents is that its use of unweighted characters means that it is independent of any prior assumptions about evolution and phylogeny — that is, it is "theory-free". Mayr (1981), however, regards this very quality as the greatest weakness of numerical phenetics if used to erect phylogenies. In other words, numerical phenetics may produce classifications of outstanding utility (for example, as aids to identification), but such classifications have no intrinsic merit in phylogenetic reconstruction unless tested against classifications erected on the basis of phylogenetically weighted characters. Conversely, Sokal & Sneath (1963) argue that phylogenetic classifications, dependent as they are on the accurate recognition of homologies and monophyletic lineages, use criteria on homology to infer phylogeny and *vice versa*, committing the logical sin of circular reasoning.

ZOOLOGICAL NOMENCLATURE

The zoological or scientific names which can be applied to animals and the manner in which they are constructed and selected are governed by a set of international rules known as the *International Code of Zoological Nomenclature*. These rules are governed and interpreted by a group of elected zoologists known collectively as **The International Commission on Zoological Nomenclature**.

What is the *International Code of Zoological Nomenclature*? What does it do and how does it work? How is it changed? And what is the function and composition of the International Commission? How are its members elected and what do they do once elected? How does the Commission communicate its opinions and how does it (or, indeed, can it) enforce them?

The modern rules of nomenclature date from the beginning of this century when, at the 5th International Congress of Zoology in Berlin in 1901, the Congress adopted the *Règles internationales de la Nomenclature zoologique* and established a Commission on Zoological Nomenclature to interpret the *Règles*. These rules were followed by most zoological taxonomists, but with many dissenters to particular requirements. At a number of subsequent International Congresses of Zoology attempts were made to up-date and revise the rules of nomenclature: abortively in Paris in 1948 (the decisions made there were never properly published and were subsequently ignored); in Copenhagen in 1953 (the Copenhagen Decisions) and in London in 1958. This latter Congress also set up an editorial committee which saw the publication, in 1961, of the *International Code of Zoological Nomenclature* adopted by the XV International Congress of Zoology — the *Code* which has applied throughout most of the working lives of the current generation of zoological taxonomists.

The bilingual (French and English) 1961 *Code* has itself been subject to a number of revisions which have been endorsed at subsequent International Congresses of Zoology. Each change has been documented fully in the *Bulletin of Zoological Nomenclature*, the serial publication of the International Commission on Zoological Nomenclature.

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A full history of the rules of nomenclature or of the people and often highly acrimonious disputes which have sometimes brought the Commission into disrepute is not appropriate to this Volume. One view of this history has been vividly presented by Blackwelder (1967).

In 1986, the Commission consists of 26 Commissioners and has a secretariat based at the British Museum (Natural History) in London. It is funded by contributions from societies and national academies in various countries, from the contributions of individual zoologists and from the sale of the Commission's publications. The principal supporting body is the London-based International Trust for Zoological Nomenclature. With the abandonment of the International Congresses of Zoology following the Monaco Congress in 1972, responsibility for the endorsement of the Commission's activities passed to the International Union of Biological Sciences which currently meets every three years.

The constitution of the Commission lays down the conditions for the election of Commissioners and their terms and duties. Most importantly, the constitution requires that the Commission be representative of a wide range of animal groups, with wide geographic coverage and of a wide range of disciplines in zoology.

In 1985, the Commission published the Third Edition of the *International Code of Zoological Nomenclature*, a major revision for which preparation began in 1973. This edition of the *Code* is also published in two languages, English and French and, like all earlier codes applies only to the names of Family-group and lower taxa, i.e. from superfamily to subspecies. The names of higher taxonomic categories are not regulated by the *Code*.

The fundamental objective of the *Code* "...is to provide the maximum universality and continuity in the scientific names of animals compatible with the freedom of scientists to classify animals according to taxonomic judgements" (Ride, 1985). In essence, the *Code* seeks to ensure that every name proposed for an animal or group of animals is ultimately based on a real organism, that it be properly and publicly described, that the appropriate name bearers be unambiguously identified and that where the same taxon has been named more than once, priority will normally be given to the first name to appear. This is done by establishing a set of rules and recommendations which lay down procedures for forming and establishing new names for those taxa which lack them or for resolving ambiguities, priorities and conflicting opinions in the application of existing names.

Significantly, the *International Code of Zoological Nomenclature*, while setting out a voluntary Code of Ethics for taxonomists, cannot enforce such a code but relies on peer pressure, professional ethics and self-interest to promote the code. Moreover, it does not attempt to impose taxonomic standards and is concerned only with the rules of nomenclature, even though poor taxonomy can have profound effects on the stability and universality of nomenclature.

Because the strict application of rules can often lead to insensitive or even absurd decisions, the *Code* provides for the use by the Commission of its plenary powers (Article 79). These powers allow the Commission, given a two-thirds majority in the vote on a particular case, to set aside the rules in that case in order to maintain a stable nomenclature.

The Third (1985) Edition of the *Code* is constructed of 18 separate chapters, together with a series of six appendices and a glossary of the terms used in the *Code*. The last two chapters deal with the powers, duties and functions of the Commission (Chapter 17) and the regulations governing the application, interpretation and amendment of the *Code*. Each

chapter is divided into two or more articles, each of which provides clear instructions, with examples where appropriate, for dealing with a particular nomenclatural issue.

There are numerous places in the present *Code* which call for different outcomes depending on the date of the nomenclatural act(s) being considered. Despite its rather legalistic language, the *Code* is not concerned with precedence. Each case brought to the Commission is considered on its own merit and only in relation to the existing *Code*.

Before discussing the *Code* and its application in any detail, there is one concept which is such a cornerstone of zoological classification and nomenclature that it warrants separate discussion.

THE CONCEPT OF TYPES

Early in the development of binomial nomenclature — certainly long before the development and wide acceptance of the Darwinian concepts of natural selection and evolution — it became clear that for any given taxon to have and retain a universal meaning or concept for all zoologists then it was necessary to establish a "standard", not unlike those established in the physical sciences for units of measurement such as the metre or the avoirdupois pound. This gave rise to the concept of a "typical" specimen(s) of each kind of animal to which all zoologists could refer as the standard for a particular species and any higher classificatory group founded on this species.

Such a standard was required for several reasons. Firstly, many original descriptions were so brief or inadequate that other zoologists had great difficulty applying the proposed name with confidence to any specimen which they had before them. Secondly, many species descriptions were based on more than one specimen; later research often demonstrated that these specimens represented more than one species and there was uncertainty as to which of these species the original name should apply. Thirdly, and most importantly, disputes concerning the correct name to be applied to any given species could be resolved only by reference to an agreed standard.

With the development of knowledge in genetics and population biology, any concept of a "typical" specimen clearly was artificial and without any basis in biology. Every individual in a population or species (except identical twins and some parthenogenetic forms) has a genetic complement different from that of every other individual. While one might be able to class a particular specimen as "average" on the basis of some arbitrary study of variation in one or more characteristics, such a classification would be meaningless in genetic terms. The original concept of a type specimen "typical" of its species, therefore, has long been abandoned.

From the mid-19th Century nomenclature has developed the use of types as a helpful device of modern systematic zoology. The type specimen and type category are reference specimens or categories which serve as standard reference points for names. In other words, the role of the type is now that of a name-bearer and the sole function of types is to resolve actual or potential problems in nomenclature by providing each name with an objective basis for its identification. In the sense, however, that species and higher categories are assigned names, and names are based on types, then type specimens and type categories continue to impinge on broad areas of zoological research and literature.

For this reason, the *International Code of Zoological Nomenclature* stresses that name-bearing types "...are the international standards of reference that provide objectivity in zoological nomenclature. They are held in trust for science by all zoologists and by persons responsible for their safe

keeping" (Article 72(g)). And, because many zoologists did not assign type status to the specimens on which they established names nor even specify the material on which their descriptions and names were based, provisions have had to be made in modern taxonomic procedures for identifying and/or designating types of such older taxa.

THE KINDS OF TYPES

The type of a species or subspecies is a specimen, while that of a higher category (such as a genus or family) is a lower category. A genus, therefore, is defined by its type species and a family by its type genus. Because the types of all higher categories are lower categories, all names ultimately are based on the lowest common denominator — the type specimen of a species or subspecies.

Not all types are necessarily name-bearers. The term "type" is also assigned as part of many compound words describing categories of specimens which are, have, or had the potential to be selected as name-bearing specimens.

The *International Code of Zoological Nomenclature* recognizes three classes of nomenclatural types:

(a) the **type series** consists of all those specimens (where there were two or more) used by an author in establishing a new species or subspecies, except those specimens which were explicitly exempted by the author, or which are excluded on other grounds specified in the *Code*. Because all of the specimens in the type series were regarded by their author as belonging to the same original taxon, then any one of them has the potential to be selected by the original or subsequent authors as a name-bearer. Once, however, the name-bearing specimen has been selected, the other specimens in the type series no longer have any greater potential role as name-bearers than specimens outside the type series.

(b) **name-bearing types** are either single specimens on which the name of a species or subspecies is based or a series of specimens each of which is equally eligible for selection as a single name-bearing specimen.

There are four kinds of name-bearing types:

(i) a **holotype** is a single specimen which is either the one designated or indicated by an author when originally establishing a species or subspecies, or was the only specimen available to that author when establishing the species or subspecies.

(ii) a **syntype** is one of two or more specimens on which an author based his or her description of a new species or subspecies, but failed to nominate any single specimen as the holotype.

(iii) a **lectotype** is one of the syntypes selected in a subsequent publication (whether by the same or a different author) to become the name-bearing specimen for the original species or subspecies.

(iv) a **neotype** is a single specimen selected and designated from any available material subsequent to the original description of a species or subspecies when there is evidence that none of the specimens available to the original author has survived and that there is no other neotype already in existence.

(c) the remaining type specimen categories are of only two kinds:

(i) **paratypes** are those specimens left in the type series after designation of a holotype.

(ii) **paralectotypes** are those specimens left in the type series after designation of a lectotype.

In all of the cases discussed above, the name-bearer for any species or subspecies is ultimately a single specimen. The nominate or nominotypical subspecies (that is, the subspecies which has the same name as its parent species) automatically possesses the same name-bearing type specimen as its parent species.

There are some kinds of animals, however, where their identity cannot be tied to a single individual. For example, colonial animals (such as corals) which exist in nature as single or discrete entities can have all or part of the colony treated as a single specimen for name-bearing purposes. Similarly, the names of many living protozoans can be interpreted only by reference to complete life cycles. In this latter case, the *Code* provides for the recognition of a **hapantotype**: one or more preparations of directly related individuals representing different stages in the life cycle.

Many other type categories have been proposed in the biological literature (e.g. topotype, homotype, allotype), some of which represent useful and functional concepts in taxonomic research. None of these, however, has any independent status as a name-bearer. Explanations of these and other type categories can be found in Mayr *et al.* (1953) and Blackwelder (1967), although attempts are still being made to modify the names of existing type categories and to introduce new ones (Fricke, 1985).

THE INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE

Following is a brief discussion of each chapter in the Third Edition of the *International Code of Zoological Nomenclature* in which only the more significant provisions of each chapter are outlined. This discussion is not an attempt to summarize the *Code*. To fully comprehend its scope and complexity it is essential that the reader consult the *Code* itself. To understand the *Code*, however, one must become familiar with some of the special meanings assigned to some everyday English words which are used widely in the *Code*. While all of these are explained fully in the Glossary of the *Code*, a helpful list of a few of the common terms is presented here:

SENIOR in the context of the *Code* refers to the oldest (*i.e.* first published) of two or more zoological names; conversely, **JUNIOR** refers to the younger (more recently published) of any two names being compared.

SYNONYMS are each of two or more names of the same rank (*e.g.* generic names) that apply to the same taxon.

OBJECTIVE SYNONYMS are each of two or more names that are based on the same name-bearing type, while **SUBJECTIVE SYNONYMS** are each of two or more names of the same rank which are considered to apply to the same taxon, but which are based on different name-bearing types.

HOMONYMS are names which are deemed to have identical spellings under the *Code*. Clearly, the use of the same name for different taxa would result in utter confusion, so the *Code* outlaws junior homonyms but allowance is made for the restitution of some junior homonyms when the homonymy is removed because of a change in generic combination.

An **AVAILABLE NAME** is one which, under the terms of the *Code*, can be applied to a particular taxon or which can, if more than one name has been applied to that taxon, compete for priority with other available names. Conversely, an **UNAVAILABLE NAME** is one that does not conform to the requirements of the *Code*; theoretically such a name should be ignored, but some taxonomists when listing names

12A. CLASSIFICATION AND NOMENCLATURE

Ctenotus pantherinus (Peters, 1866)

Lygosoma (Hinulla) pantherinum Peters, W. (1866). Eine Mitteilung über neue Amphibien (*Amphibolurus*, *Lygosoma*, *Cyclodus*, *Masticophis*, *Crotaphopeltis*) und Fische (*Diagramma*: *Hapalogenys*) des Kgl. zoologischen Museums. *Mber. K. Preuss. Akad. Wiss. Berl.* **1866**: 86-96 (89) (1867 on title page). Type data: holotype, ZMB 5379, from Swan River, W.A.

Lygosoma ocellatum Boulenger, G.A. (1896). Description of four new lizards from Roebuck Bay, north Western Australia obtained by Dr. Dahl, for the Christiania Museum. *Ann. Mag. Nat. Hist. (6)* **18**: 232-235 (233) (*non Mocoa ocellata* Gray, 1845). Type data: holotype, UZMO K2009, from Roebuck Bay, W.A.

Lygosoma ocelliferum Boulenger, G.A. (1896). *Erratum* (*Annals*, Sept. 1896, p. 233) for *Lygosoma ocellatum* read *Lygosoma ocelliferum*. *Ann. Mag. Nat. Hist. (6)* **18**: 342 (342) (nom. nov. pro *Lygosoma ocellatum* Boulenger, 1896, at that time a junior secondary homonym of *Mocoa ocellata* Gray, 1845).

Egernia whitel carnarae Kinghorn, J.R. (1931). Herpetological notes. 2. *Rec. Aust. Mus.* **18**: 85-91 (88). Type data: holotype, AM R9981, from between Canara district and North West Cape, W.A.

Lygosoma (Hinulla) brevunguis Kinghorn, J.R. (1932). Description of a new species of *Lygosoma* from northwest Australia. *Rec. Aust. Mus.* **18**: 300-301 (300 fig 1). Type data: holotype, AM R9981, from Carnarvon District, North West Cape, W.A.

available name:

junior subjective synonym
of *Ctenotus pantherinus*;
senior objective synonym of *Lygosoma*
(*Hinulia*) *brevunguis*

available name:

junior subjective synonym of
Ctenotus pantherinus;
replacement name for the unavailable
name *Lygosoma ocellatum*

unavailable name: rejected before 1961 as
a junior secondary homonym
of *Mocoa ocellata* Gray, 1845 which
in 1896 was also included in the
genus *Lygosoma*;
junior subjective synonym of *Ctenotus*
pantherinus

valid specific name:

senior subjective synonym
of all other names in this
synonymy

valid name/combination

Figure 12A.6 The status of names in part of the formal synonymy of the Ocellated Skink, *Ctenotus pantherinus*. Each name has an absolute nomenclatural status (defined by the International Code of Zoological Nomenclature and any relevant decisions of the International Commission of Zoological Nomenclature) and a relative nomenclatural status (according to taxonomic opinion). The status of each name is indicated below the formal synonymy. A VALID NAME is the correct zoological name to be applied to a particular taxon. An AVAILABLE NAME is one which meets the criteria of availability laid down in the *Code* and which can compete in priority with other available names to become a valid name; conversely an UNAVAILABLE NAME can never be used as the valid name of a taxon. A SENIOR SYNONYM is the older (earlier published) of two or more available names that are applicable to the same taxon, while a JUNIOR SYNONYM is the younger of any two available names applicable to the same taxon. An OBJECTIVE SYNONYM is one of two or more names for a taxon based on the same type, while a subjective synonym is one of two or more names applicable to the same taxon but based on different types. INCORRECT SPELLINGS, i.e. names constructed contrary to the *Code* or originally or subsequently misspelled, are not available names, but deliberately amended names (whether justified or not) are available. As it is often unclear whether an author deliberately or inadvertently introduced a different spelling, the availability of some names remains doubtful.

for taxa include unavailable names that have been given, to make their status clear and remove any doubt that they have merely been overlooked.

A VALID NAME is the correct available name, under the terms of the *Code*, to be applied to a particular taxon.

In Fig. 12A.6 is shown a SYNONYMY (that is, a list of zoological names that has been applied by the same or different researchers to the same taxon) in which are found examples of each of the categories defined above. Figure 12A.6 demonstrates the synonymy of a species. The status of each name in the synonymy is indicated and these include many of those that will be referred to in the following discussions.

Chapter 1: Zoological Nomenclature

This chapter sets out the scope and starting point for zoological nomenclature. It points out that the names of all animals known to occur in nature, both extant and fossil, fall within its boundaries. Provision is made for the inclusion of names based only on fossils that are merely impressions or replacements of the original animals, or on the fossilized work of animals (ichnotaxa) such as tracks or burrows. Conversely, names proposed for hybrids as such and some other categories are expressly excluded from the provisions of the *Code*.

The official starting date for zoological nomenclature is arbitrarily specified as 1 January, 1758. Two seminal works — the Tenth Edition of Linnaeus' *Systema Naturae* and Clerck's *Aranei Svecici* — are deemed to have been published on that date and to predate any other works published in 1758.

Chapter 2: The Number of Words in the Scientific Names of Animals

This chapter sets out the principle of binominal nomenclature for the species. It points out that the name for any species consists only of two names, that of the genus (pl. genera) which must have its first letter capitalized, and that of the species (pl. species) which must start with a lower case letter. To use our earlier example, the binominal name for the Common House Mouse is *Mus musculus*; *Mus* is the generic name and *musculus* is the specific name.

The names of all taxa above the species level consist of a single word which must begin with a capital letter (Fig. 12A.3), while those of subspecies consist of three words (a trinomen) which consists of the binomen for that particular species followed by the name of the subspecies which, like that of the species, begins with a lower case letter. Using our earlier example, *Mus musculus musculus* is the nominotypical subspecies of the Common House Mouse.

To allow for names to be used to indicate taxonomic lineages more fully, this chapter also makes provision for the interpolation into a binomen, using brackets, of the name of a subgenus or of aggregates of species or subspecies. For the purposes of the rules which regulate names of species and subspecies, none of these interpolated names is counted as one of the words in the binominal or trinominal name.

An example from the *Code*: in the birdwing butterflies of the genus *Ornithoptera* Boisduval, 1832, the species *O. priamus* (Linnaeus, 1758) is the first named member of an aggregate of vicarious species that includes also *O. lydius* Felder, 1865 and *O. croesus* Wallace, 1865. The taxonomic meaning accorded to the *O. priamus* aggregate may be expressed in the notation "*Ornithoptera* (superspecies *priamus*)" and the mem-

bers of the aggregate by the notations "*O. (priamus) priamus* (Linnaeus, 1758)", "*O. (priamus) lydius* Felder, 1865", and "*O. (priamus) croesus* Wallace, 1865".

Chapter 3: Criteria of Publication

The *Code* is concerned only with published taxonomic work and in this chapter a set of criteria is established for judging whether a particular name, or a particular nomenclatural act, has been published within the meaning of the *Code*. Some criteria are: the work in which such a name or act originally appeared must have been issued publicly for the specific purpose of providing a permanent scientific record; it must have been readily available when first issued; and it must have been produced in an edition by a method which ensured numerous identical copies. Because publishing is usually accomplished by methods which use ink on paper, until the 1985 (3rd) Edition of the *Code*, other methods were not accepted.

Quite a wide range of material clearly fails to meet these criteria under the established standards of the *Code*. Handwritten notes, photographs, microfilm, proof sheets, audio tapes, specimen labels and many theses are just some of the forms of "publishing" which are not acceptable under the *Code*.

Even more difficult to resolve is the problem created by the world-wide explosion in the use of personal computers and word-processors which, combined with the use of laser printers for type-setting and low-cost offset printing, has seen the development of rapid, quality "desk-top publishing" on an unprecedented scale. Whereas in the past, only the most wealthy members of society could afford the high cost of publishing their own work (so called "vanity publishing"), this option is now open to anyone prepared to make a modest investment in the basic computer hardware. Already the Commission is being asked to resolve conflicts arising from the private use of this new technology.

Chapter 4: Criteria of Availability

As indicated above, an available name is one which, under the terms of the *Code*, can be applied to a particular taxon or which can, if more than one name has been applied to that taxon, compete for priority with other available names. To be available, a name must meet certain essential requirements. It must have appeared in a work which consistently used binomial nomenclature and it must not have been published originally as a junior synonym except where, prior to 1961, it has been treated as an available name. Also, it must have been published after 1758, it must be written in Latin letters (e.g. not Chinese characters), whether or not it is derived from a language which uses the Latin alphabet and must be a word of more than one letter. Provided these requirements are met, a name may be formed or derived from any language, or may be an arbitrary combination of letters.

This chapter also lays down rules for Latinizing names and for automatically correcting errors in suffixes. For example, a genus-group name to be valid must be or be treated as a noun in the nominative singular, while the names of species, if Latin or Latinized words, must be nouns or adjectives.

While incorrect spellings, whether made by the original proposer of a name or by subsequent authors, are not available names, deliberately emended spellings (whether justified or not) are available unless ruled out on other criteria. However, where a first revisor has selected one of two or more dif-

ferent spellings used in an original description, then those original spellings not selected automatically become incorrect spellings and so are no longer available names.

It should also be noted that, after 1950, where new names are published anonymously they are not available.

Fortunately, another chapter of the *Code* (Chapter 7) is devoted to the formation and treatment of zoological names and the coiners of new names are helped by three of the six Appendices in the *Code* which are concerned with aspects of name construction. Appendix B lays down the procedures for the transliteration and Latinization of Greek words; Appendix C provides guidelines for the Latinization of geographical and proper names; and Appendix D contains detailed recommendations on the formation of zoological names. Helpful aids to the formation of names are manuals and lexicons such as Brown (1956) and Woods (1944).

Other fundamental requirements for a name to become available include its publication in association with "...a description or definition that states in words [those] characters that are purported to differentiate the taxon..." or "...a bibliographic reference to such a published statement" (Article 13), unless it has been expressly proposed as a new replacement name for an available name. In the case of a genus-group name, the description must be accompanied by the fixation of a type-species for the genus.

For names proposed before 1931 the requirements are less stringent, requiring if not a description or definition then at least an "indication" — a term which covers a number of quite specific situations including a combined description of a new genus and species. Nor did a genus-group name require that its type species be fixed.

In addition to these general requirements, a specific name, to become available, must also be published in combination with a generic name.

Chapter 5: Date of Publication

Because the Principle of Priority requires that the earliest (most senior) available name becomes the valid name for any given taxon, the critical issue in many cases is to ascertain which of two or more available names first appeared. The taxonomic literature in zoology is plagued by examples of names applied to the same taxon, usually by different zoologists in different countries, in the same year. Only rarely can the precise date of publication be determined, especially in the literature of the 18th and early 19th Centuries. Often, even the year of publication was not specified, or the work in which a description appeared may have been in one part of a serial work for which only the publication date of the first and/or last parts are known. Many scientific journals (even in recent decades) contain a printed publication date based on an editor's optimism rather than on a printer's actual achievement.

In this brief chapter, the *Code* sets out the manner in which a zoologist should arrive at the publication date to be adopted for publication of a name or nomenclatural act and makes provision for publication dates to be corrected when the evidence warrants it. There is a number of publications which provide the dates of publication of some significant early works, e.g. Duncan (1937) and Sherborn (1911; 1914).

Chapter 6: Validity of Names

In this chapter, the *Code* sets out two principles; the Principle of Priority and the complementary Principle of the First Reviser.

12A. CLASSIFICATION AND NOMENCLATURE

In basic form, the Principle of Priority states that where two or more available names have been applied to the same taxon, then all things being equal the oldest of those names will have priority over any others. Two points, however, must be emphasized: this principle must be used only to promote stability in nomenclature and is not to be used indiscriminately. If a taxonomist discovers that a taxon with a well-established name has an earlier, but unused available name (a senior synonym), then he or she is not to replace the younger with the older name if such an action would disturb stability or universality. Rather, the taxonomist should continue to use the well-established name while referring the matter to the Commission for adjudication.

The complementary Principle of the First Reviser states that where two nomenclatural acts or available names are published on the same date, then their precedence will be decided by the actions of the first worker who subsequently chooses to give one act or name priority over the other. This principle also applies where more than one spelling of the same name is given in the publication in which a new name is introduced. The spelling chosen by the first reviser then applies as the correct name unless there is clear evidence in the original publication that the version chosen is the wrong one.

For example, the generic name of the Pitted-shelled Turtle of southern New Guinea and northern Australia was spelt in three ways (*Carettochelys*, *Carettocchelys* and *Carretochelys*) in the original description published by E.P. Ramsay in 1886. G.A. Boulenger in 1889 subsequently chose the spelling *Carettochelys* in his *Catalogue of the Cheloniens, Rhynchocephalians and Crocodiles in the British Museum (Natural History)*. He was the first person to make the choice and is thus recognized as the "first reviser". By his act, Boulenger established *Carettochelys* as the correct spelling for this monospecific family of turtles and no other zoologist can adopt the other two spellings.

Chapter 7. Formation and Treatment of Names

This chapter sets out the standards and requirements for the selection, formation and the subsequent treatment of zoological names, dealing in turn with names of family-groups, genus-groups and species-groups. The additions of particular suffixes to the stem of the name in some taxa is declared mandatory. For example, a family name MUST end in the suffix **-idae** and a subfamily name with the suffix **-inae** (Article 29).

In the case of genus-group names, criteria are set for establishing their gender (Article 30). Greek or Latin words, or those derived from modern Indo-European languages, take the gender attributed to them in standard dictionaries. Genus-group names derived from other languages or which are merely arbitrary combinations of letters, are assigned the gender attributed by their original authors or, where no gender was originally attributed, are treated as masculine.

The importance of this provision becomes obvious in Articles 31 and 34. If a species-group name is, or ends in, a Latin or Latinized adjective or participle, then it must agree in gender with whatever generic name it happens to be combined (Article 31(b)). If such a name is transferred from a genus of one gender to that of another, its ending will change accordingly (Article 34). This requirement is often criticized for the frequent changes in spellings which it imposes and the issue is one which the Commission acknowledges as requiring resolution (Ride, 1985: xix).

For example, in Figure 26A.6 the specific name *pantherinum* is a Latin adjective and, as it was originally published by W. Peters in 1866 in combination with the neuter generic name *Lygosoma*, was given the neuter ending **-um** to agree in gender with its genus. G.M. Storr, however, in 1969 transferred Peters' species to a different genus, *Ctenotus*, which is masculine. Consequently, in its new combination the specific name must be changed to agree in gender with its new genus and so takes the masculine ending **-us**, hence its current name, *Ctenotus pantherinus*.

Species-group names which are nouns do not change their endings, however, with changes in the gender of their associated genus. Nevertheless their endings are determined by quite specific rules. For example, if a species-group name is a noun in the genitive case formed directly from a modern personal name, then it is formed by adding to its stem **-i** if the personal name is that of a man, **-ae** if it is that of a woman, **-orum** if it is of men or of one or more men and women together, and **-arum** if it is of two or more women (Article 31(a)(ii)).

For example, the Australian Sand Goanna *Varanus gouldii* was named by J.E. Gray for the famous 19th Century naturalist John Gould, whereas the colourful Gouldian Finch, *Erythrura gouldiae* was named by John Gould himself after his wife, Elizabeth Gould.

Much confusion and irritation has been generated over the use of **-i** and **-ii** endings in patronymic species-group names because it is difficult to recollect such small differences in spelling and they require constant checking. A modern personal name such as that of a man called Smith normally would become a male patronymic species-group name by the adding of **-i** to give the name *smithi*. The modern personal name, however, can be first Latinized (in this case by converting Smith to Smithius) and the name formed from it by adding **-i**. The name will then have an **-ii** ending (hence Smith → Smithius → smithii). This practice of first Latinizing modern personal names was adopted by many early taxonomists, but largely has been abandoned in this century and is not recommended by the *Code*.

Many subsequent authors ignore the second **-i** in **-ii** endings. This is not acceptable under the *Code* which, for the sake of universality, requires the correct original spellings of names to be used.

An original spelling is that spelling used in the publication in which the name was first established and this spelling is "...to be preserved unaltered unless it is demonstrably incorrect..." (Article 32(b)). There are two common situations, however, in which the original spelling requires modification.

First, if the original spelling fails to meet the grammatical and other requirements of the *Code* for the formation of names, then it must be corrected to comply with these requirements. Such corrections include the removal of hyphens (except under certain very special circumstances), diacritic marks and changing the capitalized first letter of a specific name to a lower case letter, even where such a name is derived from a proper noun.

Second, if there is clear evidence in the original publication that the name was incorrectly spelt (due, for example, to a printer's error), then this spelling too must be corrected.

In both of these cases, the modified spellings are termed "justified emendations" and, although different from those proposed by the original authors, are still attributed to them.

If the name in its original or emended form is a correct original spelling, then any subsequent changes in spelling by the same or other authors are, *ipso facto*, incorrect. These subsequent changes fall into two categories. First, are those which are deliberate changes clearly identified by their au-

thors and which are termed "unjustified emendations"; these enter the nomenclatural literature as available names with their own authors and dates. The second category includes those names which are unexplained variations of the original spelling. These are termed "incorrect subsequent spellings"; they are unavailable and so have no status in nomenclature.

One other relatively common situation is one, already dealt with, in which a new name is spelled in two or more ways in the original publication, but without any indication of which is the "correct" form. In this case, the spelling selected by the first person (the "first reviser") subsequently to apply the name deliberately to a valid taxon becomes the "correct original spelling".

Chapter 8. Family-Group Taxa and Names

This chapter defines family-group taxa as those taxonomic groupings (Fig. 12A.2) ranging above genus to the level of superfamily and propounds an important principle which applies to all taxa within this (and other) group(s). Known as the Principle of Coordination, it points out that when a name is established for any family-group taxon (which will be based on its name-bearing type — in this case, a type genus) then that name is "...deemed to be simultaneously established..." for taxa at any other rank in the family-group which is based on the same type genus.

For an example from the *Code*, the skipper butterfly family Hesperiidae, based on the generic name *Hesperia* Fabricius, was established in 1809 by Latreille (as *Hesperides*, but subsequently corrected to Hesperiidae in conformity with the *Code*). For authorship and priority, Latreille, 1809 is considered also to have simultaneously established with Hesperiidae the coordinate superfamily name Hesperioidae, the coordinate subfamily name Hesperiinae and all other names in the family group based on *Hesperia* whether or not he mentioned them at the time, even though the former was first used by Comstock & Comstock, 1904 and the latter by Watson, 1893.

There logically follows from this circumstance that when a name is raised or lowered in Rank, its type genus and its date and authorship are unchanged.

Each family-group name is based on the name of its type genus. Consequently, if a genus on which such a family-group name has been founded is later shown to be invalid because it is a synonym of an earlier name or is shown to be based on a misidentified type species, then that family-group name itself is liable to become invalid or even applied to quite a different group of animals.

Because the stability of family-group names is critical to their universality of meaning and because a long-established family-group name could be easily displaced and changed by some minor discovery of a forgotten but older name, or by minor changes in the definition of species which happen to be name-bearers of higher taxa, the *Code* makes special provision for their preservation. In essence, family-group names which won general acceptance before 1961 are maintained either by that general acceptance or, in the case of a dispute, by referral to the Commission for a decision.

After 1960, however, a family-group name is not to be replaced simply because its type genus becomes a synonym, unless other family-group names are also affected.

Chapter 9. Genus-group Taxa and Names

Genus-group taxa are genera and subgenera and they are subject to the same Principle of Coordination that applies to family-group names. The name-bearer of each genus is its

"type species", a designation which does not change even when the genus is lowered in rank to subgenus or *vice versa*. The subgenus which shares the same name and type species with its genus is called the "nominotypical subgenus" (sometimes the nominate subgenus). If, however, a generic name is shown to be invalid or unavailable, it is replaced by the next available name and its nominotypical subgenus also will have to be replaced at this time by one sharing the same name and type species.

Chapter 10. Species-group Taxa and Names

The name-bearing type of a species or subspecies is a "type specimen" (see earlier discussion on the kinds of type specimens). In this chapter, species-group names (species and subspecies) are defined. Criteria are established for deciding how to treat names proposed for ambiguous infraspecific categories such as "morph", "form", "variety" and so on.

Species-group names, as for those in other groups, are subject to the Principle of Coordination.

Chapter 11. Authorship

"The author of a name is the person who first publishes it...in a way that satisfies the criteria of availability..." (Article 50). Unfortunately, the identification of such a person or persons is not always as evident as it might be. For example, a name may have been published in a work by one author, but attributed by that author to another. Or, in a multi-authored work, whether one, all or only some of the authors were responsible for a particular name may not be clear.

It might well be asked why, if the name of an author does not form part of the name of a taxon, the *Code* should be concerned to establish authorship. Unfortunately, some of the impetus for taxonomic research derives from the satisfaction received by a taxonomist in having his or her name associated with the name of an animal in perpetuity!

This chapter sets out the criteria for deciding authorship of a name and establishes the correct forms in which authors' names should be cited. While the name of an author (and date of publication) does not form part of the name of a taxon and their use is optional, this chapter points out the advisability of doing so. The chapter also formalizes the convention for using parentheses around an author's name when the species-group name is combined with a genus (a new combination) other than the one with which its author originally combined it (original combination). This convention is independent of the subgenus with which the species name might be associated.

An example from the *Code*: the sea urchin *Goniocidaris florigera* A. Agassiz (1879), when transferred to the genus *Petalocidaris*, is cited as *Petalocidaris florigera* (A. Agassiz, 1879). If *Petalocidaris* is reduced to a subgenus of *Goniocidaris*, however, the parentheses are deleted, even when the complete citation is given as *Goniocidaris (Petalocidaris) florigera* A. Agassiz, 1879.

Chapter 12. Homonymy

The Principle of Homonymy (Article 52) provides that where two available names are identical under the *Code* (that is, they are homonyms), then the junior name (the one more recently proposed) cannot be used as the valid name for the same or any other taxon. In this chapter, this Principle of Homonymy is expounded and the criteria for establishing whether names are homonyms are set out for family-, genus- and species-group names.

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Homonyms in the family-group are those names which are identical or which differ only in suffix, but which have different name-bearing types. Homonymous genus-group names are those which also have been based on different name-bearers, but which are identical in spelling. Even a one-letter difference in spelling is sufficient to prevent two genus-group names from being homonyms.

For species-group names, two kinds of homonymy exist. If the names are identical in spelling (other than in differences in ending due to mandatory corrections for gender, or for certain variant spellings listed in Article 58) and were originally described in combination with the same generic name, then they are known as **primary homonyms**. If they were originally described in different genera but were at any time combined with the same generic name (but not necessarily contemporaneously), then they are **secondary homonyms**. Junior (younger) primary homonyms can **never** be used as the valid name for a species or subspecies and so must be replaced with the next available name or a new name if no others are available. Junior secondary homonyms replaced before 1961 are permanently rejected, but one replaced after 1960 can be reinstated if its taxon is no longer considered to belong to the same genus as that of its senior homonym.

Chapter 13. The Type Concept in Nomenclature

This chapter sets out the principle of name-bearing types, a concept whose use as a device for establishing an international "standard" for zoological names has already been discussed at length. Names which share the same name-bearing type are **objective synonyms**. Conversely, if two taxa with different name-bearing types are considered to belong to the same taxon as the result of a taxonomic revision by the action of a reviser, then they become **subjective synonyms**.

Chapter 14. Types in the Family-group

This very brief chapter establishes the role of the type genus as the name-bearer for taxa of any rank in the family-group, allows an author to choose as type genus any genus in the family-group which he or she establishes (not necessarily the oldest name) and requires that confusion caused by a misidentified type species or overlooked type species fixation be referred to the Commission for a ruling.

Chapter 15. Types in the Genus-group

In this chapter, the name-bearing type of a genus-group name is defined as the "type species" and the criteria are set out whereby such a designation, or "fixation" takes place.

The type species of a nominal genus or subgenus may be designated in several different ways. If the designation was made quite explicitly in the original publication then the type species was fixed by "original designation". If it was not designated in the original publication, but was implied by the use of a special term (such as **typus**) against one of the originally included species, then the type species is said to have been fixed by **indication**. If only one species was originally included in the genus, then that species is also fixed by indication as the type by **monotypy**. Tautonymous zoological names are those in which the name of a genus is identical with that of one of its included species or subspecies. If in the original description of a genus no type species was designated, but one of the included species or subspecies was an **absolute tautonym** of the generic name,

then that species or subspecies becomes the type species by **absolute tautonomy**. In such cases **virtual tautonyms** (*i.e.* those spelt nearly the same way) are irrelevant to the choice of a type species.

One must remember that if an author establishes a new name as a replacement name for an existing genus or proposes an unjustified emendation of an existing genus, then in both cases the new names (strictly, the new nominal taxa) automatically have the same type species as the original, irrespective of anything that the author may have stated in the publication.

If prior to 1931 the type species of a genus-group taxon was not fixed in the original publication by one of the methods described above, then the first author who subsequently designates the type species from one of the originally included species is considered to have validly fixed the type species by **subsequent designation**. After 1930, the fixation of the type species of a genus or subgenus by an author in the original description is mandatory for the name of that genus or subgenus to become available.

The assumption by the *Code* is that any author correctly identifies any existing species which he or she includes in a new genus or subgenus or designates as type species of a new or established genus or subgenus. If, however, the species is later shown in fact to be misidentified, then the *Code* requires that such a case be referred to the Commission "...to designate as the type species whichever nominal species will in its judgement best serve stability and universality of nomenclature..."

Chapter 16. Types in the Species-group

Many of the provisions of this chapter have already been covered in the previous discussion on the device of types in nomenclature. After defining the kinds of name-bearing types in the species-group, this chapter sets out the kinds of specimens that are eligible for selection as type specimens and makes a series of important recommendations concerning the accessibility, care and labelling of type specimens. As indicated previously, the name-bearing type of a species or subspecies is a single specimen which may consist of a whole animal, part of an animal, an impression, mould or cast of an animal, all or part of an asexually derived colony or, in the case of protozoans, a group of related individuals representing different stages in the life cycle.

The "type locality" is defined as the actual place of capture or collection of the type specimen(s). While subsequent authors may clarify or more accurately pinpoint the original locality than was done in the original description (perhaps from the original author's notes or museum records), the common practice of restricting a broad or generalized type locality to a more specific one based on current knowledge of the distribution of a species or subspecies has no standing in nomenclature.

The remainder of this chapter is concerned with establishing criteria whereby an author may designate lectotypes and neotype. For example, the first lectotype designation from a series of syntypes "fixes" the species or subspecies and thereby reduces the remaining syntypes to paralectotypes which can never regain syntype status even if the lectotype is lost or destroyed. Also, any subsequent attempt to designate a lectotype is invalid.

In the case of neotype, the *Code* requires that these be designated "...only in connection with revisory work, but only in exceptional circumstances when a neotype is necessary in the interests of stability of nomenclature..." (Article 75). This latter article also lays down very specific conditions which must be met before a neotype is validly designated. The

article stresses that where an original type specimen is rediscovered after a neotype has been designated, then the case is to be referred to the Commission to decide which name-bearing type is to be retained.

Chapters 17 and 18. The International Commission on Zoological Nomenclature and Regulations Governing the Code

Chapter 17 sets out the relationship between the Commission and the successors to the International Congresses of Zoology, together with the powers and duties of the Commission and the role of its Constitution and Bylaws. It also explains the status of names which are entered on the Commission's Official Lists and Indexes.

The Commission maintains and publishes four Official Indexes which cite works or names that have been rejected by rulings of the Commission. These are:

1. *Official Index of Rejected and Invalid Works in Zoological Nomenclature*
2. *Official Index of Rejected and Invalid Family-Group Names in Zoology*
3. *Official Index of Rejected and Invalid Generic Names in Zoology*
4. *Official Index of Rejected and Invalid Specific Names in Zoology*

Conversely, the Commission maintains and publishes four Official Lists which cite available works or names that have been ruled upon by the Commission. These are:

1. *Official List of Works Approved as Available for Zoological Nomenclature*
2. *Official List of Family-Group Names in Zoology*

3. *Official List of Generic Names in Zoology*

4. *Official List of Specific Names in Zoology*

Probably the most important section of this chapter deals with the Commission's **plenary powers**, powers which allow the Commission to suspend the application of any of the provisions of the *Code* in any particular case where to apply such provisions would "in its judgement" cause confusion or disturb nomenclatural stability or universality. Guiding principles for the use of the plenary powers are set out and an important provision is that where any given case is under consideration by the Commission then "existing usage" must be maintained pending the Commission's ruling. In practice, this may be difficult to achieve because in so many disputed cases the dispute arises because of different interpretations by different zoologists of what constitutes existing usage.

Chapter 18 sets out the regulations governing the use of the Third Edition of the *Code*, including its effective date of operation, its interpretation through the Glossary and the separate status of recommendations, footnotes and appendices. These latter do not form part of the "legislative text" of the *Code*.

ACKNOWLEDGEMENTS

The International Trust for Zoological Nomenclature, in which is vested the copyright of the *International Code of Zoological Nomenclature*, kindly gave permission to quote directly and indirectly from the *Code*.

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12B. MODERN TAXONOMIC CHARACTER SETS

P. R. BAVERSTOCK

INTRODUCTION

Traditionally, the reconstruction of the phylogeny of a group has been based primarily upon morphological data, often supplemented by behavioural, distributional and fossil evidence. Recently, however, with the refinement of chromosomal and molecular techniques, understanding of the phylogeny of some groups has been enhanced markedly by using such data. Unfortunately, these data are often misinterpreted and used out of context.

This Chapter gives a brief outline of the application of chromosomal and molecular techniques to phylogenetic reconstruction. The techniques themselves will be introduced only briefly. Emphasis is placed upon appropriate methods of analysis to provide realistic assessments of phylogenetic relationships from the data generated by these techniques. A more detailed discussion is given in Richardson *et al.* (1986).

THE NULL HYPOTHESIS

The number of phylogenetic trees possible for n taxa is given by the formula $1 \times 3 \times 5 \times \dots \times (2n-5)$ (Cavalli-Sforza & Edwards, 1967). This number is surprisingly large. For example, for 20 taxa there are no less than 2.2×10^{20} possible trees. This means that if you drew one million trees a second, it would still take seven million years to draw all possible trees for 20 taxa.

This raises the question of whether any one data set can possibly hope to resolve the entire tree for so many taxa. Clearly, to fully resolve such a tree, data from as many sources as possible must be used. So how can molecular and chromosomal data be utilized in this context? Rather than attempt to reconstruct totally the phylogeny of a group from a given data set, a sensible approach is to take the accepted or "traditional" phylogeny as the null hypothesis under test. Where the new data appear to contradict the null hypothesis, the question must be asked "Are the new data sufficiently strong to reject the null hypothesis?"

Such an approach has a number of significant advantages:

"Borderline" cases are seen as failing to reject the null hypothesis;

It is conservative, *i.e.* the traditional view is upheld until no longer tenable;

The new data are viewed in terms of their significance and biological relevance.

Any other approach leads to taxonomic instability and consequent chaos in systems of classification.

CHROMOSOMES

In general, the chromosome complement within a species is constant, yet often varies between species. The possibility exists, therefore, of using chromosome data for phylogenetic reconstruction.

Chromosome changes arise as mutations. Although the types of changes that can occur are many and varied, only a limited array of such changes can differentiate taxa. To become established in a lineage, any changes which occur as mutations must, at the very least, be viable in the soma and the heterozygote able to successfully undergo meiosis.

To finally reach fixation (and hence differentiate taxa), the changes must also increase in frequency due to selection or drift.

To be of value in phylogenetic reconstruction, the assessment of which chromosomes are involved in the rearrangement is important. In conventionally stained preparations, chromosomes are identified by their size and centromere position. Therefore, chromosomes of similar size and centromere position will be indistinguishable in these preparations.

In the early 1970's, various chemical treatments were found to induce transverse bands in chromosomes. The banding pattern is characteristic of a particular chromosome and is conserved over long evolutionary periods (*e.g.* Stock & Mengden, 1975; Rose & Hayman, 1985). The advent of banding allowed the identification not only of the chromosomes involved in a rearrangement, but also the precise nature of the rearrangement.

The most common types of chromosome rearrangement found to characterize taxa (Fig. 12B.1) are:

- 1) inversions;
- 2) fusions/fissions;
- 3) addition/deletion of heterochromatin.

Inversions

Inversions may be subdivided further into pericentric (where the inversion includes the centromere) and paracentric (where the inversion does not include the centromere). This distinction is necessary because paracentric inversions, unlike most pericentric inversions, will not be obvious in conventionally stained preparations. Inversions do not alter the total number of chromosomes, only the position of the centromere (see Fig. 12B.1).

Fusions/Fissions

Fusions occur when two pairs of chromosomes join. They therefore reduce the number of chromosomes by two. Fusions almost always involve the centromeres of the fusing chromosomes and are referred to as centric fusions (Fig. 12B.1). Tandem fusions involving the fusion of a centromere of one chromosome with the telomere of another chromosome do occur, but rarely characterize taxa (Fig. 12B.1). Although tandem fusions may occur commonly as mutations, they induce near total sterility in the heterozygous state and, therefore, are rarely transmitted (Lande, 1979; Baverstock *et al.*, 1982).

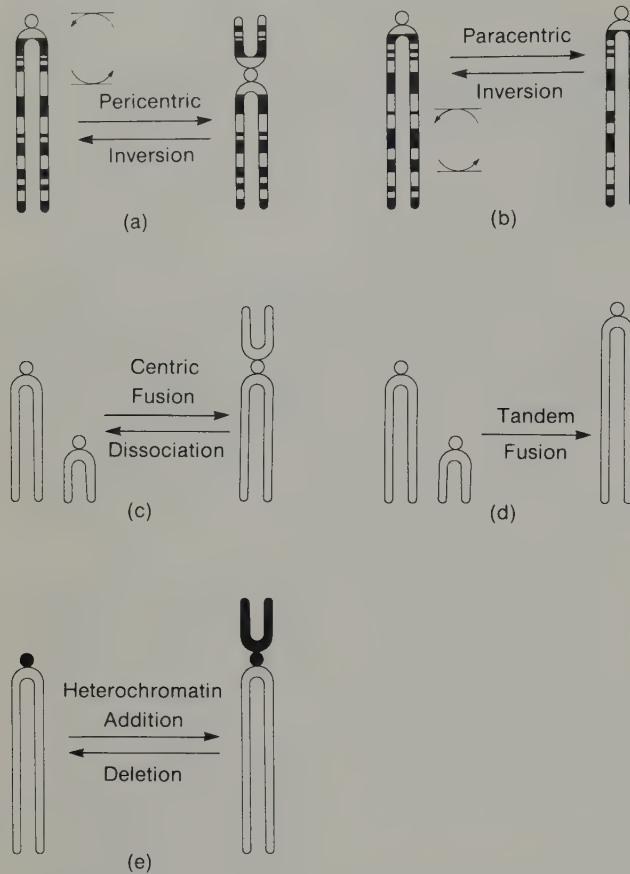


Figure 12B.1 Various types of chromosome rearrangements that can differentiate taxa; a) **Pericentric inversion**, the inversion inverts the G-banding sequence and alters the centromere position. The total chromosome number and chromosome size remain unchanged; b) **Paracentric inversion**, the inversion inverts the G-banding sequence, but does not alter the centromere position. The total chromosome number and chromosome size remain unchanged; c) **Centric fusion**, two pairs of chromosomes join at their centromeres. The total chromosome number is thereby reduced by two, but the number of chromosome arms remains unchanged; d) **Tandem fusion**, the "telomere" (free end) of one pair of chromosomes fuses with the centromere of another pair. The total chromosome number is thereby reduced by two and the number of chromosome arms is reduced by two; e) **Heterochromatic addition**, heterochromatic DNA is added to the chromosome. This is detected by differential G-banding. The chromosome size is increased. The reverse, heterochromatic deletion, also can occur.

[J. Reide]

Addition/Deletion of Heterochromatin

Heterochromatin is a special class of chromosomal material that can be visualized by specific staining techniques. In most cases, heterochromatin represents highly repeated DNA. It is commonly restricted to the centromeres. Occasionally, however, species are found that have large amounts of heterochromatic DNA amplified to form heterochromatic blocks. The amount, site and packaging of such blocks can vary enormously between closely related species, and even between populations (Baverstock *et al.*, 1977; 1982). Moreover, heterochromatin can be lost and gained over relatively short periods of evolutionary time. For these reasons, the pattern of heterochromatin distribution gives no phylogenetic information. It is, nevertheless, important to localize heterochromatin in a karyotype, since its presence can mimic other structural rearrangements in conventionally stained preparations (Fig. 12B.1).

Analysis of Chromosome Data

Chromosome data must be analysed cladistically. The plesiomorphic (ancestral) state must first be determined by outgroup analysis. Next, the "transformation series" of states must be assessed. Finally, the taxa are grouped to produce a cladogram. These steps for a hypothetical set of data are outlined in Fig. 12B.2.

There are three very important points concerning the analysis of such data.

Firstly, the common possession of the same karyotype (chromosome complement) by two or more taxa cannot be taken to indicate monophyly if that karyotype is the ancestral state for the whole group. Among the Australian marsupials, for example, wombats, pygmy possums and some bandicoots share the same karyotype. This particular karyotype, however, appears to be ancestral for the Australian marsupials, since it is shared by some South American marsupials (Rofe & Hayman, 1985). Common possession by wombats, pygmy possums and bandicoots, therefore, is not evidence for their monophyly, but is due to mutual retention of the ancestral state.

Secondly, the unique possession of a highly derived karyotype gives no useful cladistic information. Among the bandicoots, for example, all genera except *Macrotis* possess the same $2n=14$ karyotype. *Macrotis*, however, has a markedly different karyotype of $2n=19$ male and $2n=18$ female (Martin & Hayman, 1967). The *Macrotis* karyotype is so different that it is difficult to relate to the karyotype of other bandicoots. This has led some authors to conclude that *Macrotis* stands apart from the other bandicoots (e.g. Archer & Kirsch, 1977). Such a conclusion, however, is totally unjustified. Any postulated phylogenetic relationship among the bandicoots would be equally compatible with the data (Fig. 12B.3).

Thirdly, it follows that the simple fact of similarity of karyotype cannot in any way be taken to indicate closeness of relationship and, as a corollary, extensive chromosomal differences cannot be taken to indicate a distant relationship. Rates of chromosome evolution vary enormously between different groups and between different lineages within groups (Baverstock & Adams, 1986). Two taxa that are closely related (in the sense that they diverged from a common ancestor very recently) may have very different karyotypes and, conversely, two taxa that are only distantly related may possess identical karyotypes. For example, *Rattus villosissimus* and *R. colletti* are monophyletic to the exclusion of all other *Rattus* species and may be traced back to a very recent common ancestor (as evidenced by morphological, immunological and electrophoretic data), yet they show extensive karyotypic divergence (Baverstock *et al.*, 1983; 1986). *Rattus rattus* ($2n=42$ form) and *R. lutreolus*, on the other hand, are karyotypically identical, yet are only distantly related (Baverstock *et al.*, 1983; 1986).

In summary, the changes that occur in chromosomes are quantum changes rather than of a gradual nature. Moreover, any particular rearrangement is itself a rare event, so that the probability of convergence is fairly low. Chromosomes, therefore, are potentially very useful phylogenetic indicators. Because rates of chromosomal evolution vary so enormously, however, chromosome data must be viewed in a cladistic sense. The actual taxonomic level at which chromosome data are useful will also vary between different taxonomic groups.

MOLECULAR DATA

Molecular phylogenetic data can be broadly categorized into two types. The molecules studied may be the genes themselves (DNA) or gene products (proteins). Alternatively, the

molecules studied may be the endproducts of biochemical metabolism (e.g. snake venom toxins, plant phenols). The latter discipline is often referred to as **chemotaxonomy**. Because the molecules studied in chemotaxonomy are not direct gene products, it might be expected that their phylogenetic significance would be less than the strictly genetic techniques. Only the latter will be discussed here.

There seems little doubt that there is useful phylogenetic information in molecular genetic data. One of the areas of great controversy, however, is the interpretation of such data. This Section, therefore, will give only a brief overview of the principles of the techniques themselves, but present a more detailed discussion of phylogenetic analysis and biological interpretation of the data.

DNA Sequencing

Techniques exist for sequencing a given length of DNA (Maxam & Gilbert, 1977; Sanger *et al.*, 1977). Short lengths of DNA are relatively easy to sequence, but lengths the equivalent of an entire gene take much longer. To date, only one study has appeared that has sequenced the same gene in a number of related species: that for alcohol dehydrogenase in four species of *Drosophila* (Bodmer & Ashburner, 1984). The gene for alcohol dehydrogenase is a relatively short one; in the near future it is expected that improved techniques will allow DNA sequencing to be used as a routine phylogenetic tool.

DNA/DNA Hybridization

This technique assesses the extent of DNA sequence divergence between related species. There are various approaches to DNA/DNA hybridization, but all rely on the principle that the more similar are the DNAs of two species, the more readily the single stranded DNA molecules of the two species will hybridize in solution (Sibley & Ahlquist, 1983). It is a relatively simple and rapid technique.

Protein Sequencing

The technique of sequencing the amino acids of a protein is a time consuming task and is not a routinely used phylogenetic tool. Amino acid sequences, however, are known for several proteins in different taxa. Where such information is available, it can be used in phylogenetic reconstruction (e.g. Penny *et al.*, 1982).

Immunologic Techniques

These techniques involve raising antibodies to the proteins of one species and cross-reacting these antibodies to the proteins of related species. As a general principle, the strength of cross-reaction is then used as a measure of the protein similarity of the two taxa. Antisera may be raised to a mixture of proteins (polyvalent antisera – see Kirsch, 1977 for example) or to a single protein (monovalent antisera – see Champion *et al.*, 1974). When a mixture of different proteins is used, however, genetic interpretation of the data is more difficult and monovalent antisera are preferred.

Allozyme Electrophoresis

Electrophoresis can be used to separate proteins according to their electric charge. Where the same (homologous) protein has a different electrophoretic mobility in different species, the amino acid sequence (hence DNA sequence) of the two proteins must be different. The converse is not necessarily

RAW DATA SET:	TAXON:	2N
	A	42
	B	42
	C	44

PHYLOGENETIC INTERPRETATIONS:

4 possible phylogenies

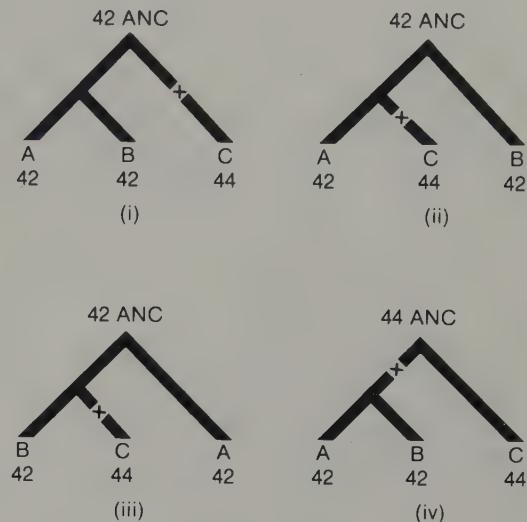


Figure 12B.2 The use of "Outgroup Analysis" for chromosome data. Three related taxa, A, B and C have 42, 42 and 44 chromosomes, respectively, which G-banding shows to be due to a centric fusion or fission (Fig. 12B.1c). In the absence of knowledge of the ancestral state for the ABC group, four phylogenies (i to iv) are all equally parsimonious, requiring one change. (The X indicates a chromosomal mutation.) If an outgroup analysis is carried out by including D, a taxon outside the ABC group but closely related to it, the ancestral condition (ANC) can be determined. If D has $2n=42$, identical to A and B, then the ANC is $2n=42$ and three phylogenies (i), (ii) and (iii) are all equally compatible with the data, i.e. require one change. If D has $2n=44$ identical to C, then ANC is also $2n=44$ and phylogeny (iv) is most compatible with the data, requiring only one change. All other phylogenies would require at least two changes. [J. Reide]

true, i.e. different proteins may have the same electrophoretic charge. In phylogenetic analysis, pairs of taxa are compared for the number of proteins of different electrophoretic mobility. A typical study would involve 30 to 40 proteins. This technique, therefore, assesses the proportion of loci that are different, without cognizance of the extent of difference for any one protein (Richardson *et al.*, 1986).

TREE BUILDING

Having amassed a set of data by one of the above methods, the next step is a phylogenetic interpretation of the data. It is in this area that so much controversy and confusion have arisen (Richardson *et al.*, 1986).

Each of the above techniques yields some estimate of genetic similarity. One might imagine that a simple "phenetic" procedure could be used. That is, the more closely related taxa are, the more similar they will be genetically. This will be true only if rates of evolution are constant for the measure being used. If they are not constant, a phenetic procedure may be totally misleading. One must appreciate why such phenetic procedures are inappropriate, since such an appre-

12B. MODERN CHARACTER SETS

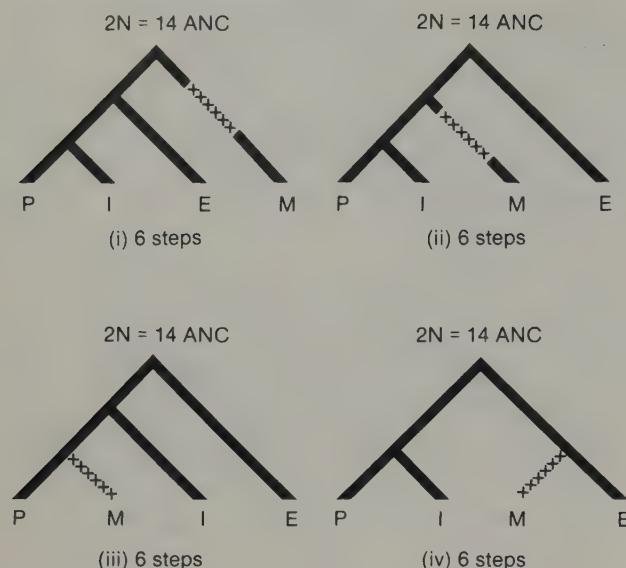


Figure 12B.3 An illustration of an "autapomorphic" chromosome complementation using the bandicoots as an example. Here, P, I and E represent the bandicoot genera *Perameles*, *Isoodon* and *Echymipera*, all of which have the $2n=14$ ancestral complement for marsupials. M represents *Macrotis lagotis*, a bandicoot with a highly derived $2n=19$ ♂, $2n=18$ ♀ complement. For the sake of argument, six changes are assumed necessary to derive the *Macrotis* complement from the ancestral complement. Here, four very different phylogenies are equally compatible with the data in requiring six steps, yet only one shows *Macrotis* standing apart from the other bandicoots.

[J. Reide]

ciation will help one understand the concepts of parsimony, maximum likelihood and minimum length so often used in the construction of phylogenetic trees.

Figure 12B.4 gives a hypothetical example where phenetic procedures would yield an erroneous conclusion. A, B and C are three taxa (say species), where A and B are monophyletic to the exclusion of C. The rate of evolution, however, is relatively fast in the branch leading to B for the character being used, be it base substitutions in DNA sequences and DNA/DNA hybridization, amino acid substitutions for protein sequences and monovalent antisera methods or the number of loci differing in an electrophoretic study. Now, for the character set used, A and C will be genetically more similar to each other than either is to B. A phenetic analysis, therefore, would show A and C to be monophyletic to the exclusion of B. The steps involved are shown in Fig. 12B.4.

Several procedures have been developed that both detect and correct for such differential rates of evolution. All involve the use of an **outgroup**. An outgroup is one or more taxa which are not themselves members of the group whose phylogeny is being assessed (the **ingroup**). The outgroup should be as closely related as possible to the ingroup and, preferably, several such outgroups should be used.

The value of an outgroup can be illustrated by reference to Fig. 12B.5. This shows the same data as in Fig. 12B.4 for taxa A, B and C, but this time including data for an outgroup, D. If rates of evolution in all of the branches leading to A, B and C were constant, then the differences between D and A, D and B and D and C would all be the same. In the example given, the distances D to A and D to C are the same, but the distance D to B is much longer. Thus, the use of the outgroup has allowed detection of the faster rate of evolution in the branch leading to B.

The next step then is to correct for the faster rate of evolution in B. One style of approach aims to minimize the distortion between the input data and the output data. To illustrate this point, refer back to Fig. 12B.4. Here, the phenetic analysis yielded a phenogram which showed both the A to B and C to B distances to be equal at 26. Yet on the input data the distances were 23 for A to B and 29 for C to B. The phenogram has thus led to some data distortion. Altering the relative branch lengths will not help. So long as A and C remain monophyletic to the exclusion of B, the data output will be a poor reflection of the data input. But, if B were made monophyletic with A to the exclusion of C and appropriate branch lengths allocated, then the fit between the input and output would be perfect.

All of the various phylogenetic methods used attempt to produce a tree that minimizes or maximizes some quantity. This is known as **parsimony**. In the example given, there were no convergences or parallelisms in the data and, indeed, any phylogenetic method would yield the correct branching relationships. The various methods differ in the way that they deal with convergences, i.e. the fundamental assumptions underlying the method.

The molecular methods described in this chapter yield data of two broad types. DNA sequencing, protein sequencing and allozyme electrophoresis yield **character state data**, whereas DNA/DNA hybridization, immunological methods and allozymes distances yield **distance data**. The hypothetical example given above treated the data as if they were distance data. Algorithms exist for determining the most parsimonious tree for either types of data. The various algorithms themselves differ in the criteria for parsimony being used. Wagner trees, for example, aim for trees of minimum length. Fitch-

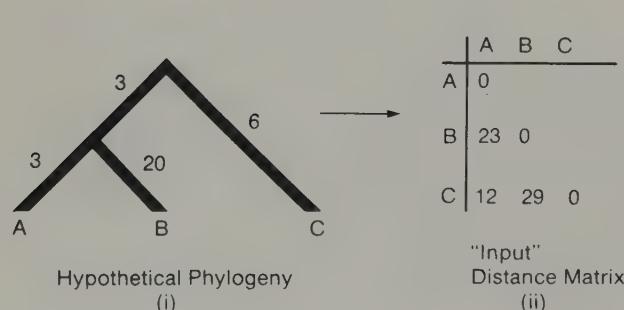
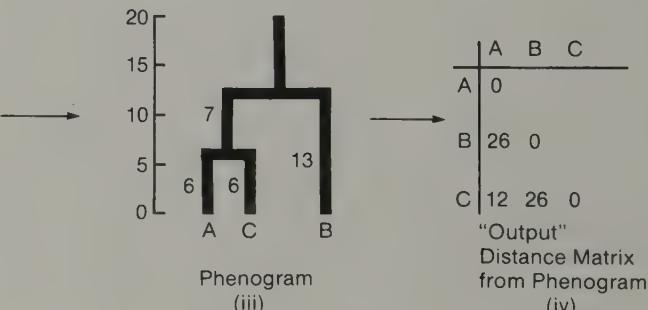


Figure 12B.4 An example of phenetic analysis of distance data leading to erroneous phylogenies; (i) Shows a hypothetical branching sequence for species, A, B and C, showing the number of changes along each branch. (ii) Shows the distance matrix that would be derived from such a phylogeny. Note that for this data set, A and C are closer than A and B. (iii) Shows the phenogram that would be derived from such a data set. (iv) Shows the "output" matrix from the phenogram. Note the differences between the "input" and "output" matrices, indicating that the phenogram is leading to data distortion.



[J. Reide]

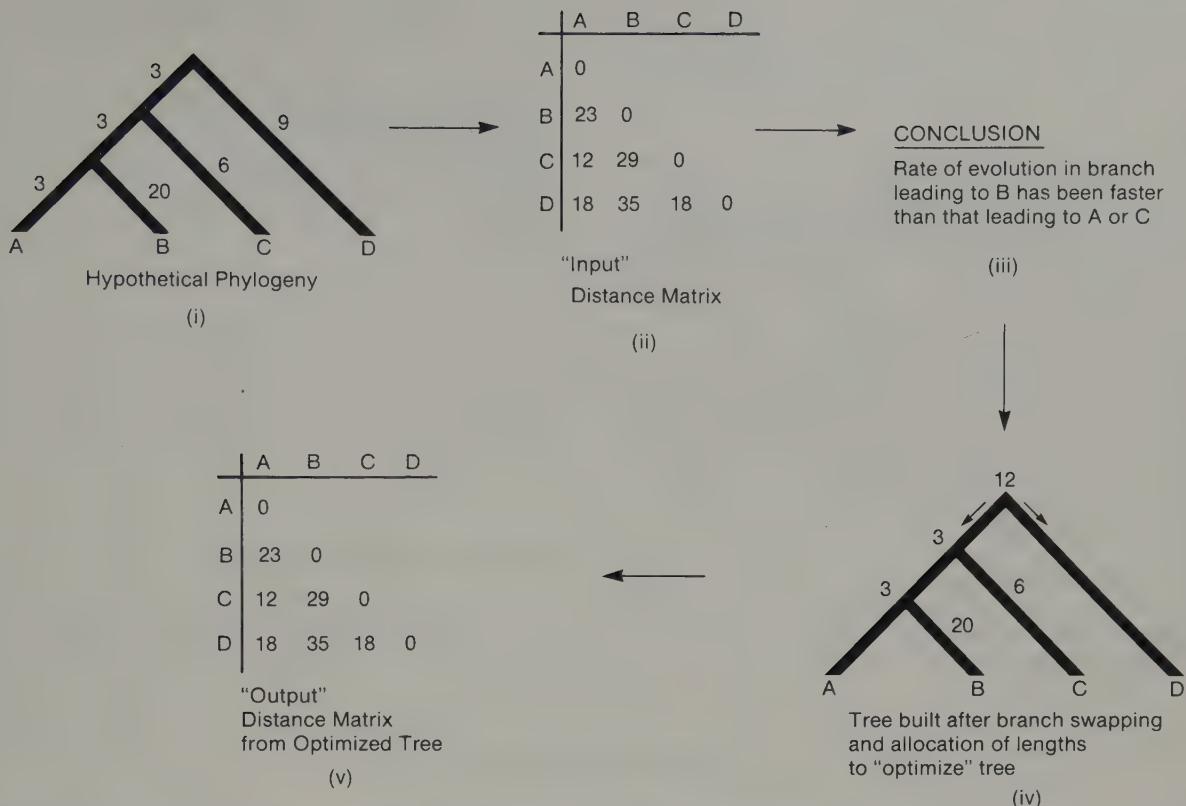


Figure 12B.5 An example of phylogenetic analysis of distance data using the outgroup approach. (i) Shows the same relationships and branch lengths as Fig. 12B.4 for three species A, B and C, but this time including an "outgroup", species D. (ii) Shows the distance matrix that would be derived from such a phylogeny. These data clearly indicate differential rates of evolution in the ABC group, at least for this data set (iii). (iv) Shows the "best-fit" tree for the data after branch-swapping and allocation of branch lengths to "optimise" the tree i.e. minimise the distortion. (v) Shows the "output" matrix. For this data set, the "input" and "output" matrices are identical, showing that there is no distortion in the tree. [J. Reide]

Margoliash trees and Prager-Wilson trees aim to minimize the difference between input and output, although using different criteria. Excellent general discussions of such methods may be found in Farris (1981), Felsenstein (1982; 1983) and in the introductory comments to the PHYLIP computer package of J. Felsenstein.

Biological Interpretation of Trees

Having derived the "best" tree by whatever criteria are used, the problem arises of biological interpretation of the tree. One would reasonably expect much of the tree to be in concord with the traditionally accepted views of the phylogeny of the group. The question that must then be asked is: "are the discrepancies sufficient to reject the traditionally held view (i.e., the null hypothesis being tested)".

For reasons outlined above, I strongly believe that only where the phylogenies generated by the new data are totally irreconcilable with the traditional view should the latter be challenged. Even then, the new view should be treated at best as a new hypothesis, on equal footing with the previous null hypothesis. Other data can then be brought to bear on the problem.

When taxa show unexpected relationships on trees, three possibilities need to be considered:

the traditional view is erroneous;

the data themselves are erroneous (always a serious consideration in biochemical taxonomy);

the tree-building procedure has led to erroneous conclusions.

The last of these can be a particularly insidious problem. It is a common experience in tree-building that some taxa behave erratically; they can be on one part of the "best" tree found, but on a completely different part on an "almost as good" tree (Colless, 1984). In this way, an apparently gross difference between the computer-generated tree and the traditional tree for the placement of one or two taxa may result.

An analysis given by Penny *et al.* (1982) illustrates the problems that can be encountered. These workers investigated the amino acid sequence data for five proteins (haemoglobin A and B, cytochrome C, fibrinopeptide A and the last 13 amino acids of fibrinopeptide B) in 11 mammalian taxa. They then used a branch and bound algorithm to search for the minimal length trees and near minimal length trees for each of the five sequences and for all sequences combined.

Penny *et al.* (1982) were using these data to illustrate a different point, but a number of conclusions relevant to the discussion can be made here.

1. The shortest trees for the five sequences were all different from each other.
2. The shortest tree for all data combined was different from any of the shortest trees for the five sequences.
3. For all data combined, two different trees were found to have a minimal length tree of 308. (One showed the horse/pig/cow/sheep clade monophyletic with the mouse/rabbit clade, while the other showed it monophyletic with the human/ape/Rhesus clade).
4. For all data combined, an additional three topologies were

12B. MODERN CHARACTER SETS

found with length 309 and six topologies with length 310.

5. Only one of the 27 minimal length or near minimal length trees for the five sequences considered individually was identical to one of the near minimal trees for all the data (it had a length of 310).

A number of observations follows:

1. The primary data base consisted of amino acid sequences. Such data would be considered among the best available;

2. This analysis considered only 11 taxa. For 11 taxa there are over 3×10^7 possible trees. Studies using biochemical procedures often consider many more taxa;

3. By their nature, many of the biochemical techniques yield distance data (e.g. immunological methods, DNA/DNA hybridization) which are invariably less suitable for tree-building. Indeed, if one takes amino acid sequence data and converts it to distance data, information is lost and the resulting trees can differ from those based on actual sequences (Romero-Herera *et al.*, 1978).

How then are such data to be handled? A sensible approach harks back to the use of the traditional view as a null hypothesis. Where the new data appear to conflict, they must be sufficiently strong to reject the null hypothesis. Where

they are sufficient, a new competing hypothesis is erected that can be tested by additional data. As Colless (1984) so succinctly puts it:

"It turns out that numerical methods may provide answers that are multiple and conflicting, or for other reasons unsatisfactory. In other words, they generate hypotheses rather than conclusions. Their role lies in exploration, not revelation".

CONCLUSIONS

Modern taxonomic character sets provide a powerful new approach to phylogenetic analysis, provided that they are treated with due caution. Chromosomal data must be analysed cladistically. Molecular genetic data must be analysed phylogenetically and the numerical analyses must be viewed conservatively.

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13. THE ANIMAL KINGDOM IN AUSTRALIA

B. J. RICHARDSON

The following synopsis of orders includes all of those orders in which marine, freshwater or terrestrial species are known from Australia or are likely to occur there. This synopsis has been developed from the results obtained during a survey of the status of taxonomic studies of the Australian fauna carried out by the Bureau of Flora and Fauna (Richardson, 1983). The information obtained on each family in that survey is summarized in Richardson (1984). The taxonomic arrangement used here is based on those given in CSIRO (1970), Margulis & Schwartz (1982) and Parker (1982) and includes alterations suggested by many of the taxonomists questioned during or since the original survey.

The Australian fauna consists of 2–300,000 species of which about 100,000 species have so far been described. These species are separable into approximately 100 classes, 400 orders and 4,000 families.

Most of the marine, freshwater and terrestrial animals of Australia can be placed into the same classes and orders used to describe the fauna in the rest of the world. The long and unique history of the continent, however (see for example Chapters 1, 3, 5, 6), has led to the evolution of some endemic orders (e.g. amongst the marsupials), while others have been lost, have never occurred here or perhaps remain to be identified and reported. At the family and lower taxonomic levels the Australian fauna is much more distinctive. Most of the terrestrial and much of the aquatic fauna are endemic at the species level.

Our knowledge of the Australian fauna is quite poor. Little is known about the identity of the animals in 70% of the orders and even less is known about aspects of their biology. Richardson (1984) shows that at least another 100 years of work are required to identify and describe the Australian fauna and that the available taxonomic expertise is concentrated on the best known groups. This taxonomic impediment (Taylor, 1983) creates a challenge facing all those interested in the survival and effective management of the Australian fauna (Anon, 1984).

A SYNOPSIS OF ORDERS

The phyla, classes and orders of animals known or presumed to occur in Australia are given. The distribution of these taxa between the 10 volumes of the *Fauna of Australia* also is shown. The status of our knowledge of each order in Australia is summarized in four categories:

Category 1 (+++), more than 75% of the species known to occur in nature are described;

Category 2 (++) , an estimated 25% to 75% of species described;

Category 3 (+), known to be present;

Category 4 (name but no symbol), undocumented, but may be present.

Groups marked with an asterisk* will be treated in the *Flora of Australia* by the Bureau of Flora and Fauna.

Fauna of Australia : Volume 10

KINGDOM: ANIMALIA

Subkingdom: Protozoa

Phylum: Sarcomastigophora

Subphylum: Mastigophora

Class: Dinoflagellata*

Class: Phytomastigophora*

Class: Zoomastigophora

Choanoflagellida	+
Kinetoplastida	+
Proteromonadida	+
Retortamonadida	+
Diplomonadida	+
Oxymonadida	
Trichomonadida	+
Hypermastigida	+
Cercomonadida	
Ebriida	

Subphylum: Opalinata

Class: Opilinatae

Opalinida

Subphylum: Sarcodina

Class: Lobosa

Amoebida	+
Schizopyrenida	+
Pelobiontida	+
Arcellinida	+
Trichosida	+

Class: Filosea

Aconchulinida	+
Gromiida	+

Class: Acarpomyxa

Leptomyxida	+
Stereomyxida	

Class: Acrasea*

Class: Eumycetozoa*

Class: Plasmodiophorea*

Class: Xenophyophorea

Psamminida	
Stannomida	

Class: Granuloreticulosa

Athalamida	
Monothalmida	
Foraminiferida	+++

Class: Acantharea

Holacanthida	+
Sympyacanthida	
Chaunacanthida	
Arthracanthida	
Actinida	+

Class: Polycystinea

Spumellarida	
Nassellarida	

Class: Phaeodaria

Phaeogymnoccidea

Phaeocystida		Heterotrichida	+
Phaeosphaerida		Odontostomatida	+
Phaeocalpida		Oligotrichida	+
Phaeoconchida		Hypotrichida	+
Phaeogromida		Subkingdom: Phagocytellozoa	
Phaeodendrida		Phylum: Placozoa	
Class: Heliozoea		Subkingdom: Parazoa	
Desmothoracida	+	Phylum: Porifera	
Actinophryida	+	Class: Demospongiae	
Taxopodida		Homosclerophorida	+
Ciliophryida	+	Astrophorida	+
Rotsphaerida	+	Spirophorida	+
Centrohelidomorph	+	Lithistida	+
Phylum: Labyrinthulata		Hadromerida	+
Class: Labyrinthulea		Axinellida	++
Labyrinthulida		Dendroceratida	+
Thraustochytriida		Dictyoceratida	+
Phylum: Apicomplexa		Verongiida	+
Class: Perkinsasida		Haplosclerida	+
Perkinsorida	+	Poecilosclerida	+
Class: Sporozasida		Halichondrida	+
Archigregarinorida		Class: Sclerospongiae	
Eugregarinorida	+	Stromatoporoida	
Neogregarinorida	+	Ceratoporellida	
Agamococcidiorida		Tabulospongida	
Protococcidiorida	+	Merliida	
Eucoccidiorida	++	Class: Calcarea	
Piroplasmorida	+	Clathrinida	+
Phylum: Microspora		Leucettida	+
Class: Metchnikovellidea		Leucosoleniida	+
Metchnikovellidida		Sycettida	+
Class: Microsporididea		Class: Hexactinellida	
Pleistophoridida	+	Amphidiscosida	+
Nosematidida	+	Dictyonina	+
Phylum: Myxozoa		Lyssacina	+
Class: Myxosporea		Subkingdom: Eumetazoa	
Bivalvulida	+	Phylum: Cnidaria	
Multivalvulida	+	Class: Scyphozoa	
Class: Actinomyxea		Stauromedusae	+
Actinomyxida		Carybdeida	+
Phylum: Ascetospora		Coronatae	+
Class: Stellatosporea		Semaeostomeae	+
Occlusosporida	+	Rhizostomeae	+
Balanosporida	+	Class: Cubozoa	
Class: Paramyxea		Cubomedusae	+
Paramyxida		Class: Hydrozoa	
Phylum: Ciliophora		Hydriida	+
Class: Kinetofragminophora		Milleporina	+
Primociliatida	+	Stylasterina	+
Karyorelictida		Trachylinida	+
Prostomatida	+	Siphonophorida	+
Haptorida		Chondrophora	+
Pleurostomatida	+	Actinulida	
Trichostomatida	+	Class: Anthozoa	
Entodiniomorphida	+	Protoalcyonaria	
Colpodida	+	Stolonifera	+
Synhymeniida		Telestacea	+
Nassulida	+	Gastraxonacea	+
Cyrtophorida	+	Gorgonacea	+
Chonotrichida	+	Alcyonacea	+
Rhynchodida	+	Coenothecalia	+
Apostomatida	+	Pennatulacea	+
Suctorida	+	Actiniaria	++
Class: Oligohymenophora		Corallimorpharia	
Hymenostomatida	+	Scleractinia	+++
Scuticociliatida		Zoanthinaria	
Astomatida	+	Ptychodactiaria	
Peritrichida	+	Antipatharia	++
Class: Polyhymenophora		Ceriantharia	+++

13. SYNOPSIS OF ORDERS

Phylum: Ctenophora		Enopliida	+
Cydippida	+	Dorylaimida	+
Platyctenida	+	Araeolaimida	+
Ganeshida	+	Chromadorida	+
Thalassocalycida	+	Desmoscolecida	+
Lobata	+	Desmodorida	+
Cestida		Monhysterida	+
Beroidea		Rhabditida	+
		Strongylida	+
		Ascaridida	+
		Oxyurida	+
		Spirurida	+
		Camallanida	+
		Tylenchida	+
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Phylum: Platyhelminthes		Phylum: Nematomorpha	+
Class: Turbellaria		Nectonematoidea	
Nemertodermatida		Gordioidea	
Acoela	+	Phylum: Acanthocephala	
Catenulida	+	Class: Archiacanthocephala	
Macrostomida	+	Oligacanthorhynchida	+
Lecithoepitheliata	+	Gigantorhynchida	+
Neorhabdocoela	+	Class: Eoacanthocephala	
Prolecithophora	+	Gyracanthocephala	
Proseriata	+	Neoechinorhynchida	+
Tricladida	+	Class: Palaeacanthocephala	
Polycladida	+	Echinorhynchida	+
Class: Trematoda		Polymorphida	+
Strigeatoida		Phylum: Arthropoda	
Aspidogastrea	+	Subphylum and Class: Crustacea	
Echinostomida	+	Notostraca	+++
Plagiiorchiida	+	Cladocera	+++
Opisthorchiida	+	Conchostraca	++
Class: Cestodaria		Anostraca	+++
Amphilinoidea	+	Myodocopida	++
Gyrocotyloidea	+	Cladocopida	+
Caryophyllidea	+	Halocyprida	++
Class: Eucestoda		Podocopida	++
Trypanorhyncha	+	Mystacocarida	
Pseudophyllidea	+	Calanoida	++
Lecanicephalidea	+	Harpacticoida	++
Aporidea	+	Cyclopoida	++
Tetraphyllidea	+	Notodelphyoida	+
Nippotaeniidea	+	Monstrilloida	+
Proteocephalidea	+	Caligoida	+
Tetrabothridae	+	Lernaeopodida	+
Cyclophyllidea	+	Acrothoracica	+
Phylum: Nemertina		Argulidea	+
Class: Anopla		Ascothoracica	+
Palaeonemertea	+	Thoracica	+
Heteronemertea	+	Rhizocephala	+
Class: Enopla		Bathynellacea	++
Hoploneumertea	+	Anaspidacea	++
Phylum: Gnathostomulida	+	Leptostraca	++
Filospermoidea		Stomatopoda	+
Bursovaginoidae		Mysidacea	+
Phylum: Mesozoa	+	Cumacea	++
Dicyemida		Tanaidacea	+
Orthonectida		Isopoda	++
Phylum: Gastrotricha		Amphipoda	++
Macrodasyida		Euphausiacea	+++
Chaetonotida		Amphionidacea	
Phylum: Rotifera		Decapoda	++
Bdelloidea	+++		
Ploimidea	+++		
Gnesiotrocha	+++		
Phylum: Kinorhyncha	+		
Cyclorhagida			
Homalorhagida			
Phylum: Nematoda			
Class: Adenophorea			

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Phylum: Arthropoda

Subphylum and Class: Crustacea

Notostraca	+++
Cladocera	+++
Conchostraca	++
Anostraca	+++
Myodocopida	++
Cladocopida	+
Halocyprida	++
Podocopida	++
Mystacocarida	
Calanoida	++
Harpacticoida	++
Cyclopoida	++
Notodelphyoida	+
Monstrilloida	+
Caligoida	+
Lernaeopodida	+
Acrothoracica	+
Argulidea	+
Ascothoracica	+
Thoracica	+
Rhizocephala	+
Bathynellacea	++
Anaspidacea	++
Leptostraca	++
Stomatopoda	+
Mysidacea	+
Cumacea	++
Tanaidacea	+
Isopoda	++
Amphipoda	++
Euphausiacea	+++
Amphionidacea	
Decapoda	++

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Subphylum: Chelicerata	
Class: Merostomata	
Xiphosura	
Class: Arachnida	
Scorpiones	++
Uropygi	++
Schizomida	
Amblypygi	+++
Palpigradi	+++
Araneae	++
Pseudoscorpionida	++
Solpugida	+
Opiliones	++
Acariformes	++
Class: Pycnogonida	+
Class: Chilopoda	
Epimorpha	+++
Anamorpha	+++
Class: Symphyla	+
Class: Diplopoda	
Peniciliata	++
Pentazonia	++
Hemimorphomorpha	++
Class: Paropoda	
Paropoda	+
Subphylum: Pentastomida	
Class: Pentastomata	
Cephalobaenida	++
Porocephalida	++

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Subphylum: Uniramia	
Class: Protura	++
Class: Diplura	++
Class: Collembola	++
Class: Insecta	
Archaeognatha	++
Thysanura	+
Ephemeroptera	++
Odonata	+++
Blattodea	++
Mantodea	++
Isoptera	+++
Orthoptera	++
Phasmatodea	++
Dermaptera	++
Embiptera	++
Plecoptera	++
Zoraptera	
Psocoptera	++
Phthiraptera	+
Thysanoptera	++
Hemiptera	++
Neuroptera	++
Megaloptera	++
Coleoptera	++
Strepsiptera	+
Mecoptera	+++
Siphonaptera	++
Diptera	++
Trichoptera	++
Lepidoptera	++
Hymenoptera	++

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Phylum: Mollusca	
Class: Monoplacophora	
Tryblidioidae	+
Class: Aplacophora	+
Class: Polyplacophora	
Lepidopleurida	+++
Ischnochitonida	+++
Acanthochitonida	+++
Class: Gastropoda	
Archaeogastropoda	++
Mesogastropoda	++
Neogastropoda	+++
Cephalaspida	++
Runcinacea	++
Acochlidacea	+
Sacoglossa	++
Doridacea	++
Dendronatacea	++
Aeolidacea	+
Aplysiacea	+++
Arminacea	+++
Notaspidea	
Thecosomata	+++
Gymnosomata	+++
Entomotaeniata	
Archaeopulmonata	
Basommatophora	++
Stylommatophora	++
Sigmurethra	
Class: Cephalopoda	
Nautiloidea	+++
Sepioidea	+++
Teuthoidea	+++
Octopoda	+++
Class: Bivalvia	
Nuculoida	+
Solemyoida	+
Mytiloida	++
Arcoida	++
Pterioida	++
Limoida	++
Ostreoida	++
Trigonioida	++
Unionoida	++
Hippuritoida	++
Venerioida	++
Myoida	++
Class: Scaphopoda	
Dentalioidea	++
Siphonodentalioidea	++

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Phylum: Onychophora	
Onychophora	+
Phylum: Annelida	
Class: Polychaeta	
Phyllodocida	+
Amphinomida	+
Spintherida	+
Eunicida	+
Orbiniida	+
Spionida	+
Chaetopterida	+
Magelonida	+
Cirratulida	+
Cossurida	+
Flabelligerida	+
Opheliida	+

13. SYNOPSIS OF ORDERS

Sternaspida	+	Phrymophiurida	++
Capitellida	+	Ophiurida	++
Oweniida	+	Class: Concentricycloidea	
Terebellida	+	Peripodida	
Sabellida	+	Subphylum: Echinozoa	
Nerillida	+	Class: Echinoidea	
Polygordiida	+	Cidaroida	++
Class: Hirudinoidea		Diadematoida	++
Rhynchobdellae	+	Echinothurioida	+
Arhynchobdellae		Pedinoida	+
Gnathobdellae	+	Phymosomatoida	++
Erpobdellae	+	Arbacioida	+
Class: Oligochaeta		Tenmopleuroidea	++
Lumbriculida	+	Echinoida	++
Tubificida	+	Holothypoida	+
Haplotaxida	++	Clypeasteroida	++
Class: Archannelida	++	Cassiduloida	+
Class: Myzostomaria	+	Spatangoida	++
Phylum: Loricifera	+	Neolampadoida	
Phylum: Priapulida	+	Class: Holothuroidea	
Phylum: Echiura		Dendrochirotida	++
Echiuroinea	++	Dactylochirotida	
Xenopneusta		Aspidochirotida	++
Heteromyota		Elasipodida	+
Phylum: Sipuncula	+++	Apodida	++
Phylum: Tardigrada		Molpadiida	++
Heterotardigrada	++	Phylum: Hemichordata	
Eutardigrada	+	Class: Enteropneusta	++
Phylum: Phoronida	+	Class: Pterobranchia	+
Phylum: Bryozoa		Phylum: Chordata	
Class: Phylactolaemata		Subphylum: Urochordata	
Plumatellida	+	Class: Ascidiacea	
Class: Gymnolaemata		Aplousobranchia	++
Ctenostomata	+	Phlebobranchia	++
Cheilostomata	+	Stolidobranchia	++
Cyclostomata	+	Class: Thaliacea	+
Phylum: Entoprocta	+	Class: Appendicularia	+
Phylum: Brachiopoda		Subphylum: Cephalochordata	+++
Class: Inarticulata		Subphylum: Vertebrata	
Lingulida	+++	Class: Agnatha	
Acrotretida	+	Petromyzoniformes	+++
Class: Articulata		Myxiniformes	+++
Strophomenida	+	Class: Chondrichthyes	
Rhynchonellida	+	Hexanchiformes	+++
Terebratulida	++	Squaliformes	+++
Phylum: Chaetognatha		Pristiophoriformes	+++
Class: Sagittoidea		Rhinobatiformes	
Phragmophora		Rajiformes	+++
Aphragmophora		Pristiformes	+++
Phylum: Pogonophora		Torpediniformes	+++
Athecanephria		Myliobatiformes	+++
Thecanephria	+	Squatiniformes	+++
Phylum: Echinodermata		Heterodontiformes	+++
Subphylum: Crinozoa		Orectolobiformes	+++
Class: Crinoidea		Lamniformes	+++
Millericrinida		Carcharhiniformes	+++
Bougueticrinida		Chimaeriformes	+++
Isocrinida	+	Class: Osteichthyes	
Comatulida	++	Osteoglossiformes	+++
Subphylum: Asterozoa		Clupeiformes	+++
Class: Stelleroidea		Elopiformes	+++
Paxillosida	++	Anguilliformes	+++
Valvatida	++	Salmoniformes	+++
Spinulosida	++	Cetomimiformes	+++
Forcipulata	++	Gonorynchiformes	+++
Oegophiurida		Cypriniformes	+++
		Siluriformes	++ +

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Phylum: Chordata	
Subphylum: Urochordata	
Class: Ascidiacea	
Aplousobranchia	++
Phlebobranchia	++
Stolidobranchia	++
Class: Thaliacea	+
Class: Appendicularia	+
Subphylum: Cephalochordata	+++
Subphylum: Vertebrata	
Class: Agnatha	
Petromyzoniformes	+++
Myxiniformes	+++
Class: Chondrichthyes	
Hexanchiformes	+++
Squaliformes	+++
Pristiophoriformes	+++
Rhinobatiformes	
Rajiformes	+++
Pristiformes	+++
Torpediniformes	+++
Myliobatiformes	+++
Squatiniformes	+++
Heterodontiformes	+++
Orectolobiformes	+++
Lamniformes	+++
Carcharhiniformes	+++
Chimaeriformes	+++
Class: Osteichthyes	
Osteoglossiformes	+++
Clupeiformes	+++
Elopiformes	+++
Anguilliformes	+++
Salmoniformes	+++
Cetomimiformes	+++
Gonorynchiformes	+++
Cypriniformes	+++
Siluriformes	++ +

Myctophiformes	+++	Pelecaniformes	+++
Polymixiiformes	+++	Ciconiiformes	+++
Gadiformes	+++	Falconiformes	+++
Batrachoidiformes	+++	Anseriformes	+++
Lophiiformes	+++	Galliformes	+++
Cyprinodontiformes	+++	Gruiformes	+++
Atheriniformes	+++	Charadriiformes	+++
Lampriformes	+++	Columbiformes	+++
Beryciformes	+++	Psittaciformes	+++
Zeiformes	+++	Cuculiformes	+++
Gasterosteiformes	+++	Strigiformes	+++
Synbranchiformes	+++	Caprimulgiformes	+++
Scorpaeniformes	+++	Apodiformes	+++
Dactylopteriformes	+++	Coraciiformes	+++
Pegasiformes	+++	Passeriformes	+++
Perciformes	+++		
Gobiesociformes	+++		
Pleuronectiformes	+++		
Tetraodontiformes	+++		
Ceratodontiformes	+++		

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Class: Amphibia	
Salientia	++
Class: Reptilia	
Testudines	+++
Squamata	+++
Crocodilia	+++
Class: Aves	
Struthioniformes	+++
Procellariiformes	+++
Sphenisciformes	+++
Podicipediformes	+++

Fauna of Australia : Volume 1B

Class: Mammalia

Monotremata	+++
Dasyurida	+++
Notoryctemorphia	+++
Peramelina	+++
Diprotodontia	+++
Chiroptera	+++
Primates	+++
Lagomorpha	+++
Rodentia	+++
Cetacea	+++
Carnivora	+++
Sirenia	+++
Perissodactyla	+++
Artiodactyla	+++

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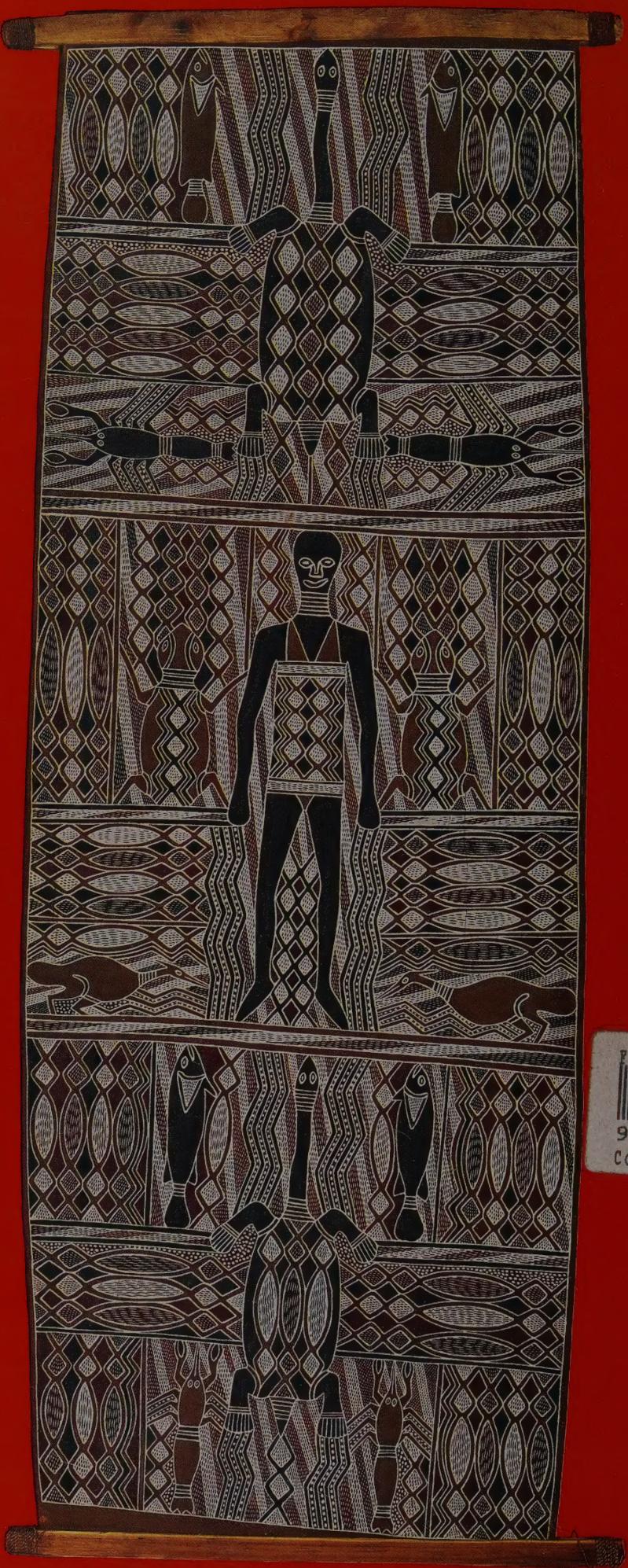
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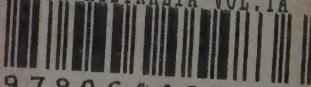
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Yangarriny Daiwangu (1932–)
Northeast Arnhem Land, Northern Territory
Ancestors of the Yirritja moiety circa 1979
ochres on *Eucalyptus* bark 155.0×56.0 cm
Collection: Australian National Gallery, Canberra



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